CLASSIFICATION OF THE TRILOBITE *PSEUDAGNOSTUS*

by JOHN H. SHERGOLD

ABSTRACT. Eighty-eight species assigned or assignable to *Pseudagnostus sensu lato* are divided into two broad divisions based on the position of the glabellar node with respect to the anterior or anterolateral glabellar furrows and anterolateral lobes. A spectaculate division, in which the node lies to the rear of the anterior furrow and to the rear of the anterolateral lobes, is divided into nine species groups which are recognized by degree of effacement of external morphology, shield shape, border morphology, glabellar morphology, pygidial spinosity, and metamerism. Three spectaculate species groups, *bulgosus*, *communis*, and *cyclopyge*, are referred to *Pseudagnostus* Jaekel, 1909, *sensu stricto*; one, *contracta*, to *Pseudagnostina* Palmer, 1962; and one, *securiger*, to *Sulcatagnostus* Kobayashi, 1937, these latter taxa being regarded as subgenera of *Pseudagnostus*. Four other spectaculate species groups, *araneavelatus*, *bilobus*, *canadensis*, and *clavus*, are classified with *Neoagnostus* Kobayashi, 1955, pending clarification of the taxonomic status and concepts of *Euplethagnostus* Lermontova, 1940, and *Pseudorhaptagnostus* Lermontova, 1940. *Hyperagnostus* Kobayashi, 1955 and *Machairagnostus* Harrington and Leanza, 1957 are synonymized with *Neoagnostus*. A papilionate division, in which the axial glabellar node lies between the anterolateral lobes and interrupts the course of the anterior furrow, consists of two species groups, *convergens* and *clarki*, which are assigned to *Rhaptagnostus* Whitehouse, 1936. The generic name *Plethagnostus* Clark, 1923 is suppressed.

THE genus *Pseudagnostus* was erected by Jaekel in 1909 for species of *Agnostus* possessing a short pygidial axis and an 'endolobe', currently termed a deuterolobe (see Öpik 1963, p. 31).

Jaekel (1909, p. 400) designated as type species *Agnostus cyclopyge* Tullberg (1880, p. 26; pl. 2, fig. 15*a*, *c*, cephalon and pygidium respectively), which occurs in the *Olenus* Zone and the zone of *Parabolina spinulosa* with *Orusia lenticularis*, at Andrarum, Skåne, and other localities in Sweden (Tullberg 1880, p. 26; Westergård 1922, p. 117; 1944, pp. 32–33; 1947, p. 22).

The type specimens, reported by Tullberg (1880, p. 26) to have been deposited in the Geological Museum, University of Lund, have not been identified. According to Dr. Jan Bergström (pers. comm. 1973), the specimens were numbered but there is no evidence that they were deposited in the type collections. Although they may not be lost, it might be difficult to differentiate them from other material in the collections from Andrarum. Until the specimens are positively located, the concept of *Pseudagnostus cyclopyge* is based on specimens collected from the type locality, figured by Westergård (1922, pl. 1, fig. 7, cephalon, Lund University Lo 3066t, and 8, pygidium, Lo 3067t), and reproduced here on Plate 15, figs. 1–2. Westergård's specimens were obtained from beds containing *O. lenticularis*.

Recent research (Öpik 1967; Shergold 1972, 1975) classifies the genus *Pseudagnostus* with Pseudagnostinae Whitehouse, 1936, which is regarded as a subfamily of Diplagnostidae Whitehouse, 1936, as emended by Öpik (1967).

When it was erected, a mere handful of species could be assigned to *Pseudagnostus*; but by now it is possible to assign no fewer than eighty-eight species, listed in Appendix B. They are united by the possession of a deuterolobe similar to that seen in the type species. Excluding this characteristic, a wide range of forms has

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been included in *Pseudagnostus*, with the result that any original concept of the genus has become substantially changed, and it has become necessary to discuss the genus in a *sensu lato* manner. This proliferation of species is directly responsible for the present review, as *Pseudagnostus sensu lato* is common in the late Cambrian of northern Australia, currently under investigation by the author. There, a range of pseudagnostinid forms spans a wide interval of late Cambrian time, and is potentially useful for the close zonation of upper Cambrian strata (Shergold 1975).

AGE AND DISTRIBUTION OF *SENSU LATO* TAXON

The time span of *Pseudagnostus sensu lato* is long: it first appears in the earliest late Cambrian (early Mindyallan *Erediaspis eretes* Zone in Australia; early Tuorian *Agnostus pisiformis*/*Homagnostus fecundus* Zone in Siberia; and early Dresbachian *Cedaria* Zone in North America) and continues into the earliest Ordovician (Canadian, *Symphysurina* and *Kainella* faunas in North America). Pseudagnostoid species are particularly common in correlatives of the late Mindyallan *Glyptagnostus stolidotus* Zone in Australia, in the late Dresbachian *Aphelaspis* and *Dunderbergia* Zones in North America, in the early Franconian and early Shidertan *Elvinia* and *Irvingella* Zones in North America and Siberia respectively, and in the late Shidertan *Lotagnostus trisectus*/*Peltura* Zone in Siberia and its equivalent post-Idamean/pre-Payntonian interval in Australia.

The genus is cosmopolitan, having lived in seas peripheral to Precambrian crustal masses now forming the nuclei of Europe, Eurasia, eastern Asia, North America, South America, Australia, and Antarctica. Within these seas, *Pseudagnostus* appears to have favoured habitats within ocean-facing environments (Palmer 1972), at the ocean–neritic boundary (Robison 1972) which approximates the boundary between carbonate belt and outer detrital belt as interpreted by Palmer (1960*a*, 1969, 1972, 1973) and Robison (1960*a*). Its species are commonly found in the deep subtidal

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EXPLANATION OF PLATE 15

Figs. 1–2. *Pseudagnostus* (*Pseudagnostus*) *cyclopyge* (Tullberg, 1880). 1, LULo 3066, topotype cephalon (Westergård 1922, pl. 1, fig. 7), ×7. 2, LULo 3067, topotype pygidium (Westergård 1922, pl. 1, fig. 8), ×7; the concept of *Pseudagnostus* currently rests on these specimens.

Figs. 3–4. *Pseudagnostus* (*Pseudagnostus*) *ampullatus* Öpik, 1967. 3, CPC 5899, paratype cephalon, ×11·5. 4, CPC 5896, holotype pygidium, ×11; an *en grande tenue* species preserved in limestone.

Figs. 5–6. *Pseudagnostus* (*Pseudagnostus*) *bulgosus* Öpik, 1967. 5, CPC 5904, paratype cephalon, ×12·5. 6, CPC 5901, holotype pygidium, ×12.

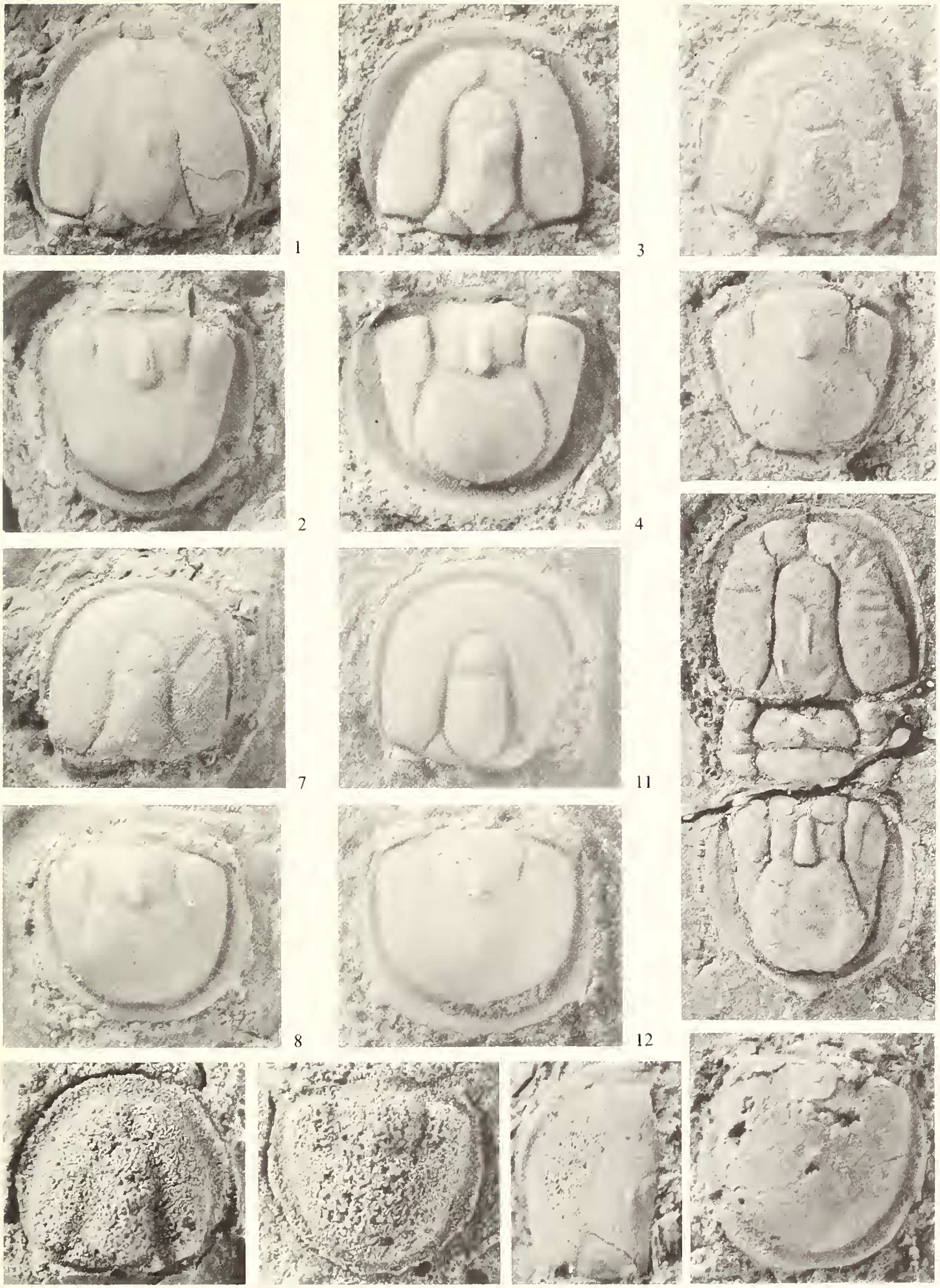
Figs. 7–8. *Pseudagnostus* (*Pseudagnostus*) *communis* (Hall and Whitfield, 1877). 7, USNM 24557e, silicone replica of hypotype cephalon (Palmer 1955, pl. 19, fig. 20), ×8·5. 8, USNM 24557d, replica of hypotype pygidium (Palmer 1955, pl. 19, fig. 21), ×12.

Figs. 9–10. *Pseudagnostus* (*Pseudagnostus*) *josepha* (Hall, 1863). 9, 10, silicone replicas of cotypes, AMNH 311, preserved as sandstone moulds, ×8; illustrated for comparative purposes.

Figs. 11–12. *Pseudagnostus* (*Pseudagnostina*) *contracta* (Palmer, 1962). 11, USNM 143149b, replica of paratype cephalon, ×16. 12, USNM 143150, replica of holotype pygidium, ×16.

Fig. 13. *Pseudagnostus* (*Sulcatagnostus*) *securiger* (Lake, 1906). GSM 57650, replica of holotype, ×6.

Figs. 14–15. *Rhaptagnostus clarki* (Kobayashi, 1935). 14, USNM 146887, paratype cephalon, ×9·5. 15, USNM 93062, holotype pygidium, ×9·5.



SHERGOLD, *Pseudagnostus*

(Laporte 1971, for terminology) outer detrital belt dark shale, silt, and finely laminated limestone deposited on the oceanic margins of carbonate banks, in deep subtidal interbank channels, and other places with current connection to the open ocean. In such environments pseudagnosti presumably contribute to late Cambrian equivalents of Agnostid Community Assemblages 1 and 2 of Jago (1973). Species of *Pseudagnostus* are also found in coarse calcarenite and debris layers, allochthonously deposited on beaches or in channels. Pseudagnosti are less commonly found in the sandstones and dolomites of the inner detrital belt (Palmer's (1960*a*, 1969, 1973) terminology). When found in inner detrital depositional environments they appear to retain a more or less constant morphology for an appreciable length of time, e.g. *P. josepha* (Hall), and are not repeatedly replaced in the biostratigraphical section by rapidly evolving taxa to the same extent as they appear to be in outer detrital and carbonate belt environments. Maximum species diversification is thus observed at the oceanic/neritic boundary, where warm shelf currents and cooler oceanic currents mingle.

MORPHOLOGY

In assessing morphology it is necessary to know if specimens are testiferous or moulds, as well as the nature of the matrix. Little information, other than the shapes of the cephalic and pygidial shields and a vague lobation and perhaps furrowing, can be gained from sandstone moulds, as is evident from the cotypes of *P. josepha* (Hall 1863) (Pl. 15, figs. 9–10). By way of contrast, the species illustrated in Plate 15, figs. 3–4 and Plate 16, figs. 3–6 demonstrate the range of morphological features shown by both exoskeletons and moulds preserved in limestone.

The distinction between morphology exhibited by moulds and by tests is basic to understanding both the reasons for the proliferation of species assigned to *Pseudagnostus*, and the difficulties in subdividing them at generic and subgeneric levels.

EXPLANATION OF PLATE 16

Figs. 1–2. *Rhaptagnostus convergens* (Palmer, 1955). 1, USNM 123563, paratype cephalon, ×10. 2, USNM 123562, holotype pygidium, ×9·5.

Figs. 3–6. *Rhaptagnostus bifax* (Shergold, 1975). 3, CPC 11596, holotype cephalon preserved with exoskeleton, ×10. 4, CPC 11656, paratype pygidial exoskeleton, ×10. 5, CPC 11597, replica of parietal surface of paratype cephalon, ×10. 6, CPC 11667, parietal surface of paratype pygidium, ×7.

Figs. 7–8. *Neoagnostus bilobus* (Shaw, 1951). 7, USNM 124467, replica of paratype cephalon, ×16. 8, USNM 124468, replica of holotype pygidium, ×12·5.

Figs. 9–10. *Neoagnostus canadensis* (Billings, 1860). 9, GSC 858, replica of paratype cephalon, ×10. 10, GSC 858b, replica of lectotype pygidium, ×9.

Figs. 11–12. *Neoagnostus araneavelatus* (Shaw, 1951). 11, USNM 124467, replica of paratype cephalon, ×20. 12, USNM 124466, replica of holotype pygidium, ×22.

Figs. 13–15. *Neoagnostus clavus* (Shergold, 1972). 13, 14, CPC 8454, paratype cephalon, lateral and dorsal views respectively, ×9. 15, CPC 8451, paratype pygidium, ×10·5.

Fig. 16. *Neoagnostus aspidoides* Kobayashi, 1955. Replica of holotype cephalon, GSC 12745, ×7.

Fig. 17. *Neoagnostus* [*Hyperagnostus*] *binodosus* (Kobayashi, 1955). Replica of holotype cephalon, GSC 12747, ×7.

Fig. 18. *Neoagnostus* [*Trinodus*] *priscus* (Kobayashi, 1955). Replica of holotype pygidium, GSC 12751, ×7·5.

SHERGOLD, *Pseudagnostus*

Some species have been described from moulds alone, others from exoskeletons, both generally in an uncritical manner. Reference to Plate 15, figs. 3–4 will show that supposedly diagnostic differences may readily be found if preservation is ignored. When such differences become the basis for generic taxa, obvious problems arise.

In an earlier paper (Shergold 1975), and here, a major distinction is made between the morphology of the outer surface of the exoskeleton, and that of its internal surface. The latter can be observed directly on the inner surface of silicified or phosphatized exoskeletons; most commonly, however, it is interpreted from impressions on the surface of its internal mould. Such surfaces are here termed 'parietal surfaces', and their morphology, which is a negative of the inner surface of the exoskeleton, is termed 'parietal morphology'.

From the classificatory point of view, the morphology of the outer surface of the exoskeleton gives information on lobes and furrows, and the positions of nodes and spines. Parietal morphology, on the other hand, gives basic anatomical information relating to the internal musculature, and the vascular and caecal systems of the organism, as deduced from the occurrence and distribution of various scrobiculations, muscle scar impressions, and pits.

Morphological terminology applicable to Pseudagnostinae (*inter alia*) has been defined exhaustively elsewhere (Öpik 1963, 1967; Shergold 1972, 1975). Terminology used in the classification presented here, and not readily evident from these papers or requiring further comment, is summarized in Appendix A.

LOCATION OF MATERIAL

Observations on personally collected Australian specimens have been supplemented by the acquisition of replicas of the types of most established taxa, and the study of museum materials in Europe, North America, and Japan.

Located material is in the collections of repositories abbreviated as follows:

AMNH	American Museum of Natural History, New York, U.S.A.
BMNH	British Museum (Natural History), London, U.K.
BYU	Brigham Young University, Provo, Utah, U.S.A.
CPC	Commonwealth Palaeontological Collection, Canberra, A.C.T., Australia.
GMAN	Geological Museum, Kazakhstan Academy of Science, Alma Ata, U.S.S.R.
GSC	Geological Survey of Canada, Ottawa, Canada.
GSCh	Geological Survey of China, Peking, China.
GSM	Institute of Geological Sciences, London, U.K.
HAN	Cambrian Catalogue, Geological Survey, Hanover, Germany.
IGAL	Institute of Arctic Geology, Leningrad, U.S.S.R.
IGGN	Siberian Research Institute for Geology, Geophysics, and Mineral Raw Materials (SNIIGGIMS), Novosibirsk, U.S.S.R.
IGUT	Institute of Geology, University of Tokyo, Japan.
IPP	Institute of Palaeontology, Peking, China.
LU	Laval University, Quebec, Canada.
LULo	Lund University, Lund, Sweden.
MCZ	Museum of Comparative Zoology, University of Harvard, Cambridge, Massachusetts, U.S.A.
MNHU	Museum für Naturkunde, Humboldt University, East Berlin, D.D.R.
MSM	Manchurian Science Museum, Mukden, Manchuria, China.

NHMM	Natural History Museum, Mendoza, Argentina.
NUP	National University, Peking, China.
NZAR	Athropod Register, New Zealand, Geological Survey, Lower Hutt, New Zealand.
OGM	Oklahoma Geological Survey, Tulsa, Oklahoma, U.S.A.
OUM	Oxford University Museum, Oxford, U.K.
RMS	Riksmuseet, Stockholm, Sweden.
SGU	Geological Survey of Sweden, Stockholm, Sweden.
THU	Tsing-hua University, Peking, China.
UBA	University of Buenos Aires, Argentina.
UQ	University of Queensland, St. Lucia, Queensland, Australia.
USGS	United States Geological Survey, Washington, D.C., U.S.A.
USNM	National Museum of Natural History (formerly United States National Museum), Washington, D.C., U.S.A.
UT	University of Texas, Austin, Texas, U.S.A.
YPM	Peabody Museum, Yale University, New Haven, Connecticut, U.S.A.
ZSGU	Museum of the West Siberian Geological Board, Novokuznetsk, U.S.S.R.

CLASSIFICATION

For the purposes of this review species assigned to the following closely related or synonymous genera and subgenera were considered: *Pseudagnostus* Jaekel, 1909; *Plethagnostus* Clark, 1923; *Rhaptagnostus* Whitehouse, 1936; *Sulcatagnostus* Kobayashi, 1937*a*; *Pseudorhaptagnostus* Lermontova, 1940; *Euplethagnostus* Lermontova, 1940; *Neoagnostus* Kobayashi, 1955; *Hyperagnostus* Kobayashi, 1955; *Machairagnostus* Harrington and Leanza, 1957; and *Pseudagnostina* Palmer, 1962. These species, together with others previously classified elsewhere, are listed in Appendix B. Three other pseudagnostinid genera were examined but are not considered further in the classification: *Litagnostus* Rasetti, 1944, because of the extreme difficulty in assessing this very effaced form; *Xextagnostus* Öpik, 1967, because of its uncharacteristically simple articulating device and different pygidial diverticular structure; and *Oxyagnostus* Öpik, 1967, because of its distinct deuterolobe morphology which cannot be confused with that of *Pseudagnostus* (see Öpik 1967, pp. 159–161).

For the purposes of classification the most obvious differences between species are carapace shape and degree of effacement. Less obvious, but seemingly more important from the anatomical point of view, is the position of the axial glabellar node with respect to the anterior furrow and anterolateral glabellar furrows. Species fall broadly into two divisions. Spectaculate pseudagnosti are those in which the glabellar node lies to the rear of the anterolateral lobes. Two groups are discernible: those in which the anterior furrow is transverse, straight, or gently curved backwards and the anterolateral lobes are distinctly separated sagittally, e.g. *Pseudagnostus communis* (Hall and Whitfield), as refigured by Palmer (1955) (see Pl. 15, figs. 7–8); and those in which the anterior furrow is V-form, and the anterolateral lobes meet, and may fuse, sagittally, e.g. *Neoagnostus bilobus* (Shaw, 1951) (Pl. 16, fig. 7). Papilionate pseudagnosti are those in which the node interrupts the course of the anterior furrow, dividing it into V-form anterolateral furrows, and lies between the anterolateral lobes as, for example, in *Rhaptagnostus clarki* (Kobayashi, 1935*a*) (Pl. 15, fig. 14).

An intermediate condition, in which the node interrupts the course of the anterior furrow, dividing it into V-form anterolateral furrows, but still lies slightly behind the anterolateral lobes, is included within the spectaculate division of this classification, but could possibly be regarded as a distinct category. The condition appears to be gradational, but the observed differences could be interpreted as the result of preservation.

The spectaculate condition embraces the bulk of species assigned to *Pseudagnostus sensu lato*. Spectaculate pseudagnosti occur earlier, being first found in the earliest late Cambrian of Australia, North America, and Siberia, and disappear later, in the early Ordovician of North America. The intermediate forms occupy a relatively narrow time interval during the late Cambrian, in the *Elvinia* and *Conaspis* Zones and their correlatives in Europe, Siberia, and Australia. Papilionate pseudagnosti arise during this time interval, at least in Australia (Shergold, in prep.), and continue into the earliest Ordovician (in Mexico). Thus there appears to be a time-related forward migration of the axial glabellar node.

The function of the axial glabellar node is not known: nor is the reason for its apparent migration. Some speculation may, however, be offered. Parietal surfaces of some pseudagnostinid cephala show the axial and terminal glabellar nodes connected by an axial carina which itself bears a longitudinal sulcus (Shergold 1975, pl. 3, fig. 5; text-fig. 15), structures which can be interpreted as having supported the gut and a dorsal tubular heart. The high spot of the axial glabellar node is frequently perforated, particularly in limestone moulds. Ruedemann (1916) interpreted the glabellar node of *Cryptolithus* as a dorsal median eye containing a single fluid lens, and such lenses may have occupied the perforated regions of both cephalic and pygidial axial nodes in agnostids, their function being to assess the intensity and direction of light and orient the animal within the water column. Harris and Mason (1956) have shown that experimentally blinded *Daphnia* are 'more sensitive to light than normal ones and show a greater capacity for adaptation to light during the cycle of vertical migration' (p. 285). Thus the lack of a compound eye, also lacking in agnostids, is no bar to photokinesis. Harris and Mason (1956) have suggested for *Daphnia* an interrelationship of the photosensitive system, the nervous system, and reflex control of the heart rate. The cephalic and pygidial nodes of pseudagnosti may well, therefore, be connected with photosensitive systems in direct connection with the blood vascular system, the combination facilitating orientation and migration of the animal in the water column.

Öpik (1961*a*, p. 417) has considered that the agnostid stomach consists of anterior and posterior sacs connected by a constricted passage beneath the anterior transverse glabellar furrow. In pseudagnosti, however, the lateral portions of this furrow merely represent the internally raised anterior margins defining the anterolateral muscle attachment areas which, depending on the length of muscle, would not necessarily constrict the stomach. Any interruption or modification of the course of the anterior furrow, as is apparent, is therefore more likely to reflect a modification of the muscle attachment areas. The positioning of the axial glabellar node between the anterolateral muscle attachment areas in papilionate pseudagnosti may have resulted in the lateral separation of the bases of the appendages attached there, and/or restricted the area of attachment of such appendages, which would presumably be restricted in size. This situation may be contrasted with that seen in the spectaculate species here assigned to *Neoagnostus*, in which the attachment areas may meet axially. The anterolateral muscle scars are generally the largest of the pseudagnostinid cephalon, and are thought to represent the areas of attachment for mandibular appendages. Thus modification of the shape and position of the mandibular attachment areas could reflect difference in feeding habit. Hence this classification is based on anatomical features fundamental to the animal.

While the position of the axial node and its relationship to the anterolateral muscle scars is regarded here as basic in the classification of Pseudagnostinae, other factors are of considerable value in recognizing species groups. Some can be recognized by degree of effacement, whereas in others this characteristic varies presumably in response to environmental conditions. Ideally species groups should comprise taxa in which the condition of effacement is relatively constant, and in practice this is difficult to attain owing to the differing preservation exhibited by established species. Ideally genera should embrace effaced, partially effaced, and *en grande tenue* species groups.

Degree of effacement influences observation on the condition of other characteristics used in this classification. Although all pseudagnosti are deuterolobate, as deduced from parietal morphology, the degree of tumidity of the deuterolabe and degree of incision of its associated bounding accessory furrows vary considerably. Externally effaced and partially effaced pseudagnosti are generally weakly deuterolobate and non-plethoid parietally. Species externally *en grande tenue* are usually strongly deuterolobate and plethoid, but there are exceptions, e.g. the *bilobus* species group described below. In similar manner degree of deliquiation (Shergold 1975) is related to effacement. Externally effaced and partially effaced species are non-deliquiate or subdeliquiate: their moulds are likely to have subdeliquiate and deliquiate marginal furrows. *En grande tenue* species are deliquiate, and their moulds strongly so: generally cephala are more strongly deliquiate than their assigned pygidia.

Carapace shape, which may be subcircular, subovoid, subquadrate, or subrectangular, is relatively constant in some, but not all, species groups. Pygidial segmentation, which can be assessed from the number of muscle scars and apodemes on the internal surface of the test, or the number of muscle-scar impressions and notulae on the parietal surface, may be related to shield shape. As a generalization, elongated pygidia have more paired muscle attachment areas, and by inference segments, than subquadrate ones. Similarly, the position of the posterolateral pygidial spines may be related to the shield shape: elongate pygidia have anteriorly situated spines with respect to the termination of the deuterolobe, whereas subquadrate pygidia have retrally sited spines. Shield shapes, and consequently spine positions, may change during morphogenesis. Most species in which meraspid pygidia have been observed have a subquadrate shield with retrally positioned spines. Change in shape occurs with the development of the deuterolobe during late meraspid morphogenesis (see Palmer 1955, pp. 94–96, pl. 20 for *P. communis*).

Morphological features associated with the anterior portion of the pygidial axis have not been fully exploited in this classification. While the clarity of the transverse furrows, and the axial furrows bounding the pre-deuterolobe axis is dependent on the degree of effacement shown by the exoskeleton in general, the degree of anterior divergence of the axial furrows varies considerably, even within species. Among some species assigned here to *Neoagnostus*, a third pair of muscle scars is consistently enclosed by axial furrows. In others, their visibility is dependent on degree of effacement, cf. *N. bilobus* (Shaw) (Pl. 16, fig. 8) and *N. araneavelatus* (Shaw) (Pl. 16, fig. 12), and manner of preservation (exoskeleton or mould). A third pair of muscle-scar impressions is often also visible on exfoliated specimens of *Pseudagnostus* and *Rhaptagnostus*, but in these is never bounded by axial furrows (e.g. Pl. 16, fig. 2). The characteristic is variable, but may have some use in differentiating isolated pygidia of *Neoagnostus* from those of *Pseudagnostus* or *Rhaptagnostus*.

The position of the pygidial axial node is quite variable, but unlike the axial glabellar node this variation is inconsistent. It lies across the sagittal length of the second axial segment, is apparently connected to the axial region between the muscle scars of the first segment, and extends rearwards between the scars of the third segment to varying extents. In *Pseudagnostus* and its subgenera, it terminates generally at the front of the third intermuscle scar area (Pl. 15, figs. 2, 4, 6, 10, 13); in *Rhaptagnostus* it may extend considerably further between the third pair of muscle scars (Pl. 16, figs. 2, 6); but in *Neoagnostus* its extent is only consistent within individual species (cf. Pl. 16, figs. 8, 10, 12, 15). Size, shape, and transverse separation of the muscle scars evidently influence observation of the extent of this feature.

In many pseudagnosti the axial pygidial node is bilobed, having anterior and posterior high spots (see Pl. 15, figs. 4, 6; Pl. 16, figs. 2, 6), and is bifid, being posteriorly cleft (Pl. 16, fig. 6). On some specimens the anterior high spot is perforated, like the axial glabellar node. The axial pygidial node is therefore a complicated structure which presumably had multiple functions.

DELINEATION OF SPECIES GROUPS

Species are grouped here on the combinations of characteristics listed above. Considerable variation occurs in some of the groups whereas others are quite homogeneous. The groups are not species, although synonymous species may exist within them. Species groups may constitute subgenera, but apart from those lying at the limits of variation, e.g. possessing three pygidial spines (*securiger* group) or are extremely effaced (*contracta*), for which names are already available (*Sulcatagnostus* and *Pseudagnostina* respectively), it is preferred not to name them formally at this time. Not all species have yet been examined at first hand, particularly Russian taxa, and some may further modify the concepts presented herein.

Of the species listed those marked with an asterisk signify that type or subsequently figured material has been examined in museum collections, or from silicone replicas.

A. SPECTACULATE PSEUDAGNOSTI

Araneavelatus group (Pl. 16, figs. 11–12)

Nominal species. **Pseudagnostus araneavelatus* Shaw, 1951, pl. 24, p. 113, figs. 12–16, holotype pygidium USNM 124466, paratype USNM 124467, remainder untraced, early Ordovician, *Missisquoia* Zone, Vermont, U.S.A.

Diagnosis. Cephalon subcircular, *en grande tenue* or partially effaced, non-deliquiate or subdeliquiate, spectaculate, tendency to develop prominent furrows to the rear of the anterolateral lobes, anterolateral furrows generally externally effaced, median preglabellar furrow absent. Pygidium subcircular, partially effaced, non-deliquiate, non-plethoid, weakly deuterolobate, spines posteriorly situated close to a transverse line drawn across the rear of the deuterolobe, possibly eight late holaspid metameres.

Other species

**Pseudagnostus coronatus* Shergold, 1975, pp. 85–87, pl. 6, figs. 1–6, holotype cephalon CPC 11692, paratypes CPC 11693–11697.

Pseudagnostus cyclopygeformis (Sun) *sensu* Kobayashi 1960, p. 341, pl. XIX, fig. 6, IGUT no number, *non* fig. 7 (*clarki* group), IGUT no number.

**Phalacroma cyclostigma* Raymond, 1924, p. 397, pl. 12, fig. 4, holotype pygidium YPM 4747.

**Pseudagnostus denticulatus* Shergold, 1975, pp. 87–89, pl. 8, figs. 1–5, holotype cephalon CPC 11705, paratypes CPC 11706–11709.

**Pseudagnostus* sp. *C* Shergold, 1975, pp. 91–92, pl. 7, figs. 5–7, CPC 11714–11716.

Age and distribution. Late Cambrian: pre-Payntonian/post-Idamean, *Rhaptagnostus clarki patulus* with *Caznaia squamosa* through *R. bifax* with *Neoagnostus denticulatus* Assemblage-Zones (Shergold 1975), western Queensland, Australia; late Changshanian; *Kaolishania* Zone, Tanggok, South Korea.

Early Ordovician; *Missisquoia* Zone, Vermont, U.S.A.

Comments. The Australian species listed here as constituting the *araneavelatus* group were previously placed in the *clavus* group (Shergold 1975). They are nevertheless distinguishable from the *clavus* and *bilobus* groups (below) by their rounded shield shapes and proportions. The arrangement of glabellar lobes and furrows shown is common to all groups.

Bilobus group (Shergold 1975, p. 92) (Pl. 16, figs. 7–8)

Nominal species. **Pseudagnostus bilobus* Shaw, 1951, pp. 112–113, pl. 24, figs. 17–22, holotype pygidium USNM 124468, paratypes USNM 124469–124471, early Ordovician, *Missisquoia* Zone, Vermont, U.S.A.

Diagnosis. Cephalon subquadrate, generally *en grande tenue*, deliquiate or subdeliquiate, spectaculate, tendency to over-deepen furrows both in front and behind the anterolateral glabellar lobes; a median preglabellar furrow is generally present. Pygidium subcircular or subquadrate, partially effaced, deliquiate or subdeliquiate, non-plethoid, weakly deuterolobate, spines generally sited on a transverse line across the rear of the deuterolobe or behind it; a third pair of muscle-scar impressions is incorporated into the axis behind and adjacent to the pygidial axial node.

Other species

**Neoagnostus aspidoides* Kobayashi, 1955, pp. 473–474, pl. VII, fig. 5, holotype cephalon GSC 12745, *non* fig. 4, geragnostoid pygidium GSC 12746, pl. IX, fig. 5 (line-drawing).

**Hyperagnostus binodosus* Kobayashi, 1955, p. 475, pl. VII, fig. 2, holotype cephalon GSC 12747, *non* fig. 3, geragnostoid pygidium GSC 12748, pl. IX, fig. 4 (line-drawing).

Agnostus cyclopyge Tullberg *sensu* Sun 1939, p. 30, pl. 1, figs. 1–3, repository and numbers not known.

**Pseudagnostus longicollis* Kobayashi, 1966, p. 283, fig. 7, IGUT no number.

**Trinodus priscus* Kobayashi, 1955, p. 476, pl. VII, fig. 6, holotype pygidium GSC 12751.

**Pseudagnostus quasibilobus* Shergold, 1975, pp. 94–95, pl. 12, figs. 1–7, holotype cephalon CPC 11717, paratypes CPC 11718–11723.

Machairagnostus tmetus Harrington and Leanza, 1957, p. 64, figs. 6–7, holotype (complete specimen) UBA 1297, paratypes UBA 1195, 1292–1294, 1298.

*Undetermined pseudagnostid, Robison and Pantoja-Alor 1968, p. 780, pl. 97, fig. 23, USNM 158886.

Age and distribution. Late Cambrian: Payntonian, *Neoagnostus quasibilobus* with *Tsinania nomas* Assemblage-Zone (Shergold 1975), western Queensland, Australia; Fengshanian, Yunnan; Wanwanian, Jehol Block, China.

Early Ordovician: Oaxaca Province, Mexico; *Missisquoia* Zone, Vermont, U.S.A.; Tremadocian, *Parabolina argentina* Zone, Argentina; *Missisquoia*, *Symphysurina*, and *Kainella–Evansaspis* faunas, British Columbia, Newfoundland, Canada.

Comments. Like the *clavus* group from which it is possibly derived, the *bilobus* group represents an assemblage of species linked through the orientation of their glabellar furrows. Cephala are, in general, preserved *en grande tenue*, whereas pygidia have depressed deuterolobes and effaced accessory furrows. The retral position of the pygidial spines is constant among the species cited.

Bulgosus group (Pl. 15, figs. 5–6)

Nominal species. **Pseudagnostus bulgosus* Öpik, 1967, pp. 156–158, pl. 38, fig. 8; pl. 62, figs. 1–4, Mindyallan zones of *Erediaspis eretes* and *Glyptagnostus stolidotus*, western Queensland, Australia. Designated holotype pygidium CPC 5901, paratypes CPC 5902–5904, 5656.

Diagnosis. Cephalon subovoid, *en grande tenue*, spectaculate, deliquiate, anteriorly converging acrolobe, median preglabellar furrow absent. Pygidium subovoid, *en grande tenue*, convergent flanks, subdeliquiate, plethoid, deuterolobate, restricted pleural lobes, very small spines in advance of a transverse line drawn across the rear of the deuterolobe in holaspides.

Other species

**Oedorhachis boltonensis* Resser, 1938, p. 50, pl. 10, figs. 19–20, cotypes USNM 94869.

Pseudagnostus levatus E. Romanenko *in* Romanenko and Romanenko, 1967, pp. 75–76, pl. 1, figs. 18–19, holotype pygidium ZSGU 133/135, paratype ZSGU 133/136.

**Oedorhachis mesleri* Resser, 1938, p. 50, pl. 10, figs. 13–14, cotypes USNM 94864.

**Pseudagnostus nganasanicus* Rosova, 1964, pp. 27–28, pl. 16, figs. 3–4, holotype pygidium IGGN 113/875, paratype IGGN 113/928.

Possibly also included in the *bulgosus* group is:

Pseudagnostus mestus Öpik, 1967, pp. 155–156, pl. 62, figs. 5–6, holotype pygidium CPC 5906, paratype cephalon CPC 5905.

Age and distribution. Late Cambrian: Mindyallan, *Erediaspis eretes* and *Glyptagnostus stolidotus* Zones, western Queensland, Australia; Dresbachian, *Cedaria* Zone, Virginia and Tennessee, U.S.A.; Tuorian, zones of *Agnostus pisiformis* with *Homagnostus fecundus* and *Glyptagnostus stolidotus*, Kulyumbe River, Katun River, and Lena River, Siberian Platform, U.S.S.R.

Comments. This is the earliest species group referable to *Pseudagnostus sensu lato*, homogeneous in content and character.

Canadensis group (Pl. 16, figs. 9–10)

Nominal species. Agnostus canadensis Billings, 1860, p. 304, fig. 3*a–b*, lectotype pygidium (designated Rasetti (1944) GSC 858b, paratype cephalon GSC 858, refigured as *Pseudagnostus canadensis* (Billings), (Rasetti 1944, p. 234, pl. 36, figs. 8–13, GSC 858, 858b, LU 1104a–d), late Cambrian, Lévis Conglomerate, Quebec, Canada.

Diagnosis. Cephalon subquadrate, *en grande tenue*, wide borders with deliquiate marginal furrows, spectaculate, anterolateral glabellar furrows effaced, but those to rear of anterolateral lobes prominent, median preglabellar furrow present parietally. Pygidium subquadrate, *en grande tenue*, wide borders with deliquiate marginal furrows, strongly deuterolobate, strongly plethoid, restricted pleural areas, retral spines.

Other species. Rasetti (1944) has synonymized *Agnostus janei* Clark, 1923, p. 124, fig. 8; 1924, p. 19, fig. 5, MCZ 1696.

Age and distribution. Late Cambrian: Lévis Conglomerate, Quebec, Cow Head Group conglomerates, Newfoundland (C. H. Kindle, pers. comm.).

Comments. The *canadensis* group is readily recognized by its strongly *en grande tenue* condition and fused anterior and anterolateral glabellar lobes. Most probably it has been derived from the same ancestral stock as the *araneavelatus* group.

Clavus group (Shergold 1975, p. 82) (Pl. 16, figs. 13–15)

Nominal species. **Pseudagnostus clavus* Shergold, 1972, pp. 31–34, pl. 3, figs. 1–8, holotype pygidium CPC 8453, paratypes CPC 8451, 8454–8456; also Shergold, 1975, pp. 84–85, pl. 8, figs. 6–12, CPC 11689–11704, late Cambrian, *Rhaptagnostus bifax* with *Neoagnostus denticulatus* and *R. clarki maximus* with *R. papilio* Assemblage-Zones (Shergold 1975), western Queensland, Australia.

Diagnosis. Cephalon subquadrate, *en grande tenue* or partially effaced, wide borders with subdeliquiate or deliquiate marginal furrows, spectaculate, prominent V-form anterolateral glabellar furrows, weakly chevronate furrows to rear of anterolateral lobes, rhomboid anterior lobe, median preglabellar furrow absent, proximally present, or present. Pygidium subquadrate to subovoid, *en grande tenue* or partially effaced, non-deliquiate or subdeliquiate, non-plethoid or subplethoid, generally weakly deuterolobate, retral pygidial spines, seven to eight metameres in late holaspides.

Other species

**Rhaptagnostus acutifrons* Troedsson, 1937, pp. 22–24, pl. 1, fig. 9, RMS number not known.
**Pseudagnostus cavernosus* Rosova, 1960, pp. 12–14, pl. 1, figs. 1–4, holotype pygidium IGGN 76/557, paratype 74/556; holotype refigured Rosova *in* Khalfin 1960, p. 165, pl. Cm-XVIII, fig. 4.
Pseudorhaptagnostus punctatus Lermontova, 1940, p. 126, pl. 49, fig. 14, 14*a*, repository and numbers not known.
Pseudorhaptagnostus simplex Lermontova, 1951, pp. 12–13, pl. 2, figs. 11–15, *non* figs. 16–17, designated holotype is pygidium fig. 11, repository and numbers not known; also *Pseudagnostus simplex* (Lerm.) *in* Nikitin 1956, pl. XIV, fig. 5, *non* fig. 4.
Euplethagnostus subangulatus Lermontova, 1940, p. 126, pl. 49, fig. 15, 15*a*, repository and numbers not known.
**Pseudagnostus vulgaris* Rosova, 1960, pp. 14–16, pl. 1, figs. 5–13, holotype pygidium IGGN 76/645, paratypes IGGN 74/524, 75/582, 76/578, 76/647, 76/653, 76/654, 76/656, 79/633; refigured Rosova *in* Khalfin 1960, p. 165, pl. Cm-XVIII, fig. 5*a–c*.
**Pseudagnostus* sp. *A* Shergold, 1975, pp. 89–90, pl. 7, figs. 1–2, CPC 11710–11711.
**Pseudagnostus* sp. *B* Shergold, 1975, pp. 90–91, pl. 7, figs. 3–4, CPC 11712–11713.

Questionably belonging to this group are:

**Homagnostus* cf. *acutus* Kobayashi, 1938, pp. 173–174, pl. XV, fig. 4, cephalon GSC 11979.
Pseudagnostus bituberculatus Ivshin *in* Khalfin, 1960, p. 165, pl. Cm-XVIII, fig. 6*a–b*, repository and numbers not known.
Pseudagnostus quadratus Lazarenko, 1966, pp. 46–47, pl. 1, figs. 24–29, holotype cephalon IGAL 36/8907, paratype numbers not known.

F

Age and distribution. Late Cambrian: post-Idamean/pre-Payntonian, *Rhaptagnostus clarki patulus* with *Caznaia squamosa* through *R. c. maximus* with *R. papilio* Assemblage-Zones (Shergold 1975), western Queensland, Australia; Shidertan, zones of *Irvingella* to *Lotagnostus trisectus/Peltura* (Ivshin and Pokrovskaya 1968), Kazakhstan, Sayan Altai, Olenek River, U.S.S.R.; early Franconian, *Elvinia* Zone, British Columbia, Canada; Changshanian, *Kaolishania* Zone, South Korea; late Cambrian, Tienshan, China.

Comments. As presently constituted, this is a heterogeneous group that varies considerably in degree of effacement and deliquiation, and somewhat in shield shape. Species are presently linked in possessing a V-form anterior glabellar furrow, rhomboidal anterior lobe, and seven or eight pygidial metameres. Many Russian species are, however, inadequately known and may be wrongly classified within this group. Possibility exists for further dividing the group on presence or absence of a median preglabellar furrow. As far as is known only Australian representatives lack a well-defined median preglabellar furrow externally.

Communis group (Palmer 1968, p. 30) (Pl. 15, figs. 7–8)

Nominal species. *Agnostus communis* Hall and Whitfield, 1877, pp. 228–229, pl. 1, figs. 28–29, late Cambrian, Dunderberg Shale, locality unknown, Nevada, *sensu* Palmer (1955, pp. 94–96, pl. 19, figs. 20–21, USNM 24557).

Regardless of synonymy, many specimens have been referred to *Pseudagnostus communis* (Hall and Whitfield), viz:

*Palmer, 1954, pp. 720–721, pl. 76, figs. 1–3, UT 32205, USNM 123309, UT 32169.
*Palmer, 1960*b*, p. 61, pl. 4, figs. 3–4, USNM 136832a–b.
*Robison, 1960*b*, p. 14, pl. 1, figs. 2, 5, BYU 10911-0-975a–b.
*Rasetti, 1961, p. 109, pl. 23, figs. 13–17, USNM 143054–143055.
Bell and Ellinwood, 1962, p. 389, pl. 51, figs. 7–21, UT 34842–34856.
*Lochman, 1964, p. 47, pl. 9, figs. 32–36, USNM 140664a–e.
*Rasetti, 1965, p. 39, pl. 10, figs. 23–25, USNM 144547.
*Palmer, 1968, pp. 29–30, pl. 7, figs. 5, 10, USNM 136832a–b.

Diagnosis. Cephalon subcircular to subovoid, partially effaced, narrow borders with non-deliquiate or subdeliquiate marginal furrows, spectaculate, anterior glabellar furrow usually transverse rectilinear, median preglabellar furrow invariably present. Pygidium subcircular to subovoid, partially effaced, subplethoid, weakly to strongly deuterolobate, narrow borders with subdeliquiate marginal furrows, spines well in advance of a transverse line drawn across the rear of the deuterolobe, eight late holaspid metameres.

Other species

**Agnostus coloradoensis* Shumard, 1861, p. 218, cephalon USNM 26928.
**Pseudagnostus convergens* Palmer *sensu* Lochman and Hu 1959, p. 412, pl. 57, figs. 1–6, USNM 137088a–f.
**Agnostus josepha* Hall, 1863, p. 178, pl. 6, figs. 54–55; 1867, p. 169, pl. 1, figs. 54–55; refigured *in* Shimer and Shrock, 1944, pl. 251, figs. 5–6, cotypes AMNH 311.
**Pseudagnostus josephus* (Hall) [*sic*] *sensu* Grant 1965, p. 108, pl. 13, figs. 13–14, USNM 142409–142410.
**Pseudagnostus* cf. *P. laevis* Palmer *sensu* Grant 1965, p. 108, pl. 14, figs. 34–35, USNM 142319.
**Pseudagnostus latus* Kobayashi, 1938, p. 171, pl. XVI, figs. 23–24, cotypes GSC 11989–11990, ?*non* figs. 40–41, GSC 11991–11992.
**Agnostus neon* Hall and Whitfield, 1877, pp. 229–230, pl. 1, figs. 26–27, cotypes USNM 24568; refigured Palmer 1955, pp. 94, 96, pl. 19, figs. 16, 19, and synonymized with *communis*.
**Pseudagnostus orientalis* Kobayashi, 1933, pp. 98–99, pl. IX, figs. 20–22, IGUT unnumbered [holotype fig. 22]; 1935*b*, pp. 110–111, pl. III, figs. 7–11, 23, IGUT unnumbered.

**Agnostus prolongus* Hall and Whitfield, 1877, pp. 230–231, pl. 1, figs. 30–31, cotypes USNM 24637; refigured Palmer, 1955, pp. 98–99, pl. 19, figs. 17, 22.

**Pseudagnostus prolongus* (Hall and Whitfield) *sensu* Lochman and Hu, 1959, pp. 412–413, pl. 57, figs. 7–16, USNM 137089a–k.

**Pseudagnostus* cf. *prolongus* (Whitfield) [*sic*] *sensu* Lochman and Hu, 1960, p. 812, pl. 95, fig. 36, USNM 138218.

Pseudagnostus rotundatus Lermontova, 1940, p. 125, pl. 49, fig. 12, 12*a–c*, repository and numbers not known.

Pseudagnostus rotundatus Lermontova *sensu* Pokrovskaya *in* Tchernysheva *et al.* 1960, p. 464, pl. 2, fig. 7, repository, numbers, and location (apart from Siberia) unknown.

**Pseudagnostus sentosus* Grant, 1965, pp. 108–109, pl. 9, figs. 2–3, 5, holotype pygidium USNM 142284, paratypes USNM 142283, 142434.

**Pseudagnostus vulgaris* Rosova *sensu* Palmer, 1968, p. 30, pl. 12, fig. 5, USNM 146845, ?*non* fig. 6, USNM 146661.

**Pseudagnostus* spp., Palmer, 1962, p. 21, pl. 2, figs. 16, 21, 26, USNM 143147a–b, 143148.

**Pseudagnostus* sp., Robison and Palmer, 1968, pp. 169–170, photo 3, USNM 158031.

Questionably included in the *communis* group are also:

**Pseudagnostus gyps* (Clark) *sensu* Rasetti, 1959, p. 381, pl. 51, figs. 13–14, USNM 136929.

Pseudagnostus cyclopygeformis (Sun) (*pars*) *sensu* Endo *in* Endo and Resser, 1937, p. 316, pl. 65, figs. 19–22, *non* pl. 68, figs. 8–16, MSM 1080, 1157, 1249, 1260, 2582 (unplaced).

Age and distribution. Late Cambrian: late Dresbachian zones of *Aphelaspis*, *Dicanthopyge*, and *Dunderbergia*; Franconian zones of *Elvinia*, *Conaspis* (*Taenicephalus*), *Ptychaspis* (*Idahoia*), and *Saukia* (*Illaenurus*), Nevada, Utah, Texas, Idaho, Montana, Wyoming, Alabama, Wisconsin, Minnesota, Maryland, Tennessee, Alaska, U.S.A.; *Elvinia* Zone, British Columbia, Canada; late Tuorian, zone of *Glyptagnostus reticulatus*; Shidertan, zone of *Plicatolina perlata*, Yakutia, Olenek River, U.S.S.R. (Lazarenko 1966; Ivshin and Pokrovskaya 1968); Paishanian, *Chuangia* Zone, Liaotung and Taitzuho, Manchuria, and South Korea.

Comments. A *Pseudagnostus communis* species group initially was recognized by Palmer (1968, p. 30), although no unifying or diagnostic characteristics were listed. The assignment of species made here differs from those listed by Palmer.

As constituted here, the *communis* group exhibits variation in shield shape and to some extent the position of the axial glabellar node. Species intermediate between spectaculate and papilionate exist, e.g. *P. communis sensu* Rasetti, 1961, *P. neon* (Hall and Whitfield), and the specimens ascribed to *P. prolongus* by Lochman and Hu (1959), which appear to link the *communis* group morphologically to that of *Rhaptagnostus clarki* (following). Within a single paradigm there is a more or less constant degree of effacement.

Contracta group (Pl. 15, figs. 11–12)

Nominal species. **Pseudagnostina contracta* Palmer, 1962, p. F21, pl. 2, figs. 18–20, 22–25, holotype pygidium USNM 143150, paratypes USNM 143149a–b, 143151–143152, 143153a–b, late Cambrian, Dresbachian, *Cedaria* Zone, Nevada, Alabama, U.S.A.

Diagnosis. Cephalon subovoid to subquadrate, effaced or partially effaced, deliquiate and subdeliquiate marginal furrows, strongly spectaculate, rectilinear transverse anterior furrow, median preglabellar furrow absent. Pygidium subovoid to subquadrate, effaced or partially effaced, subdeliquiate marginal furrows, non-plethoid, weakly deuterolobate, spines variable but usually posteriorly positioned close to the rear of the deuterolobe.

Other species

**Pseudagnostina vicaria* Öpik, 1967, pp. 158–159, pl. 55, fig. 4; pl. 63, figs. 8–9, holotype pygidium CPC 5918, paratypes CPC 5816, 5919.

**Pseudagnostina*? sp. indet. (aff. *vicaria* sp. nov.) Öpik, 1967, p. 159, pl. 63, fig. 10, CPC 5920.

Öpik (1967, p. 150) has noted that species described as *Agnostus douvillei* Bergeron by Walcott (1913, p. 100, pl. VII, fig. 3, 3*a*–*b*; pl. XI, figs. 6–7) and Resser and Endo (*in* Endo and Resser 1937, p. 162, pl. 49, figs. 25–28) may belong to *Pseudagnostina*. *A. koerferi* Monke (1903, pp. 111–114, pl. 3, figs. 1–9; pl. 9; Woodward 1905, pp. 211–215, 251–255, pl. 13, fig. 5), synonymized with *douvillei* by Walcott (1913, p. 100), thus may also belong to *Pseudagnostina*. Wolfart (1974, p. 90) has synonymized other references to *A. douvillei* (Mansuy 1916; Kobayashi 1935*b*; Lu 1957; Lu *et al.* 1965), with his *Pseudagnostus kobayashii*, which is tentatively included here in the *cyclopyge* group. The type cephalon of *A. douvillei* Bergeron (1899, p. 503, pl. XIII, fig. 3, repository and number unknown), cannot be readily interpreted. The species *Oedorhachis boltonensis* Resser, which Palmer (1962, p. 21) regarded as belonging to *Pseudagnostina*, is here placed in the *bulgosus* species group.

Age and distribution. Late Cambrian: Mindyallan, *Glyptagnostus stolidotus* Zone, western Queensland, Australia; Dresbachian, *Cedaria* Zone, Alabama, Nevada, U.S.A.; Kushanian, *Drepanura–Stephanocare* interval, Vietnam, China (Shantung), Manchuria (Liaotung), South Korea.

Comments. This group may represent an effaced derivation from the *bulgosus* group.

Cyclopyge group (Pl. 15, figs. 1–2)

Nominal species. **Agnostus cyclopyge* Tullberg, 1880, p. 26, pl. II, fig. 15*a*, *c*, as interpreted by Westergård 1922, pp. 116–117, pl. 1, figs. 7–8 (LULo 3066t–3067t), late Cambrian, zones of *Olenus* and *Parabolina spinulosa* with *Orusia lenticularis*, Andrarum, Skåne, Sweden (see discussion in introduction to this paper). Of other specimens which have been assigned to this species, the following have been traced:

**Agnostus cyclopyge* Tullberg *sensu* Lake 1906, pp. 27–28, pl. II, figs. 21–22, OUM number not known and BMNH 58494 respectively; also **Pseudagnostus cyclopyge* (Tullberg) *sensu* Rushton *in* Taylor and Rushton 1971, p. 26, pl. VIII, figs. 1–2, GSM Ru1202, 1042.

Diagnosis. Cephalon subovoid to rounded subquadrate, *en grande tenue*, wide borders with strongly deliquiate marginal furrows, spectaculate, subovoid to subcircular acrolobe, transverse rectilinear anterior furrow in early representatives becoming curved backwards or V-form in later ones, median preglabellar furrow present. Pygidium subovoid to rounded subquadrate, *en grande tenue*, wide borders with strongly deliquiate marginal furrows, plethoid, deuterolobate, spines generally well forwards of a transverse line across the rear of the deuterolobe.

Other species

**Pseudagnostus ampullatus* Öpik, 1967, p. 150, pl. 61, figs. 7–11, holotype pygidium CPC 5896, paratypes CPC 5897–5900.

Pseudagnostus angustilobus Ivshin, 1956, pp. 19–21, pl. 9, figs. 11–15, 18–23, holotype cephalon GMAN 69/926, paratypes GMAN 73/926, 68/926, 72/926, 78/926, 79/926, 85/926, 84/926, 83/926, 123/926, 84/926.

Agnostus chinensis Dames, 1883, pp. 27–28, pl. 2, figs. 18–19; Kobayashi 1937*b*, p. 434, pl. 17, fig. 14*a*–*b*, material destroyed; Schrank 1974, pp. 622–623, pl. 1, figs. 1–7, MNHU K302, T893.2, 893.3, 894.1, 895.1; *non Agnostus chinensis sensu* Walcott, 1913, pp. 99–100, pl. 7, figs. 4–5; *non Pseudagnostus chinensis* (Dames) *sensu* Lu *et al.* 1965, p. 41, pl. 4, figs. 3–5 = *Peronopsis rakuroensis* (Kobayashi) *fide* Kobayashi (1937*b*, p. 434).

Pseudagnostus communis (Hall and Whitfield) *sensu* Lu *et al.* 1965, pp. 41–42, pl. 4, figs. 6–8, repository and numbers not known.

Homagnostus convexus Chu, 1959, pp. 88–89, pl. 1, figs. 3–4, *non* figs. 1–2, 5–7, also *in* Lu *et al.* 1965, p. 20, pl. 1, fig. 10, *non* figs. 8–9, IPP 9411–9412.

**Pseudagnostus* cf. *cyclopyge* (Tullberg) *sensu* Whitehouse, 1936, p. 100, pl. X, fig. 8, UQ F3188; probably equivalent to *Pseudagnostus* cf. *vastulus* Whitehouse *sensu* Öpik, 1963, pp. 50–53, text-fig. 13, CPC 4302.

**Pseudagnostus idalis* Öpik, 1967, p. 153, pl. 62, figs. 8–9; pl. 63, figs. 1, 3, holotype pygidium CPC 5908, paratypes CPC 5909–5911, 5913.

**Pseudagnostus* cf. *idalis* Öpik, 1967, p. 154, pl. 63, fig. 4, CPC 5914.

**Plethagnostus jarillensis* Rusconi, 1953, p. 4 [*nom. nud.*]; 1954, pp. 19–20, fig. 6, holotype pygidium NHMN 16674.

**Pseudagnostus leptoplastorum* Westergård, 1944, p. 39, pl. 1, fig. 1, holotype pygidium SGU C459; also *P. leptoplastorum* Westergård *sensu* Ivshin, 1962, pp. 16–18, pl. 1, figs. 8–18, GMAN 646/105–107, 110, 113–117, 120, 124.

**Pseudagnostus marginisulcatus* Kobayashi, 1962, p. 32, pl. III, figs. 10–11, holotype cephalon, paratype pygidium IGUT, unnumbered.

**Pseudagnostus nuperus* Whitehouse, 1936, p. 100, pl. X, figs. 5–7, holotype cephalon UQ F3199, paratypes UQ F3200–3201.

**Agnostus obtusus* Belt, 1868, pp. 10–11, pl. II, figs. 15–16 [fig. 15, not located, fig. 16 BMNH 58494].

**Pseudagnostus primus* Kobayashi, 1935*b*, pp. 108–109, pl. XIV, figs. 6–10, IGUT, unnumbered (fig. 6 designated holotype cephalon); also Kobayashi, 1962, pp. 31–32, pl. III, figs. 15–17, pl. V, figs. 8–12, IGUT, unnumbered.

Pseudagnostus pseudocyclopyge Ivshin, 1956, pp. 17–19, pl. 1, figs. 1–8, 10, 16–17, holotype cephalon GMAN 74/926, paratypes GMAN 64/926, 66/926, 121/926, 70/926, 75/926, 83/926, 80/926, 77/926, 87/926, 86/926; Ivshin 1962, p. 18, pl. 1, figs. 19–22, GMAN 646/217, 646/125, 646/123.

**Pseudagnostus sericatus* Öpik, 1967, pp. 152–153, pl. 62, fig. 7, holotype cephalon CPC 5907.

**Pseudagnostus* sp. undet., Shergold *in* Shergold *et al.* 1976, pp. 264–265, pl. 41, figs. 9–11, NZAR 601–603.

The *cyclopyge* group possibly also includes:

Pseudagnostus kobayashii Wolfart, 1974, pp. 90–93, pl. 10, fig. 8; pl. 11, figs. 3–7, HAN 82/1, 82/2, 83/1, 84/2 (synonymy given).

**Oedorhachis tennesseensis* Resser, 1938, p. 50, pl. 10, figs. 24–26, cotypes USNM 94871.

**Pseudagnostus vastulus* Whitehouse, 1936, pp. 99–100, pl. X, figs. 3–4, holotype pygidium UQ F3203, paratype UQ F3202.

Pseudagnostus sp., Lu 1956*b*, pp. 367–368, pl. 1, figs. 1–2, ?IPP 8643–8644; also *in* Lu *et al.* 1965, p. 43, pl. 4, figs. 18–19, same repository and numbers.

Age and distribution. Late Cambrian: zones of *Parabolina spinulosa*, *P. brevispina*, *Leptoplastus rhaphidophorus*, and *Peltura scarabaeoides*, United Kingdom, Sweden; late Tuorian, *Glyptagnostus reticulatus* Zone; early Shidertan, *Irvingella* Zone, central Kazakhstan (Ivshin and Pokrovskaya 1968); Kushanian, *Blackwelderia paronai* fauna, Manchuria; late Kushanian, Afghanistan; Paishanian, *Chuangia* Zone, China (Kweichow), *Eochuangia* Zone, South Korea; late Mindyallan, *G. stolidotus* Zone, Idamean zones of *G. reticulatus* with *Proceratopyge nectans*, *Corynexochus plumula*, *Erixanium sentum*, and *Irvingella tropica* with *Agnostotes inconstans* (Öpik, 1963, 1967), western Queensland, Australia. Species of the group also occur in South America (Argentina), where their age is uncertain; in Antarctica (northern Victoria Land) of probable late Idamean age (Shergold *et al.* 1976); and possibly in North America (Tennessee), early Dresbachian, *Blountia* Zone (Resser 1938).

Comments. The *cyclopyge* group is heterogeneous and probably capable of further division. Its members exhibit some variation in shield shape, degree of effacement, orientation of anterior glabellar furrow, extent of pygidial pleural lobes, and strength, shape, and orientation of the pygidial spines. Early species are distinctly spectaculate, but later Cambrian ones may begin to approach the papilionate condition, in that the axial glabellar node migrates forwards and begins to interfere with the anterior furrow without actually coming to rest between the anterolateral lobes. The *cyclopyge* group grades with effacement into the *communis* group.

Securiger group (Pl. 15, fig. 13)

Nominal species. **Agnostus securiger* Lake, 1906, p. 20, pl. II, fig. 11, GSM 57650, late Cambrian, *Olenus* Zone, Outwood Shales, Chapel End, near Nuneaton, Warwickshire, U.K.

Diagnosis. Cephalon subovoid to subquadrate, *en grande tenue*, spectaculate, deliquiate marginal furrows, subovoid acrolobe, transverse rectilinear anterior glabellar furrow, median preglabellar furrow present. Pygidium subovoid to subrounded, *en grande tenue*, deliquiate marginal furrows, strongly deuterolobate, plethoid, posterolateral spines in advance of a line drawn across the rear of the deuterolobe plus a third sagittal spine developed from the posterior margin.

Other species. No other species are described, although a trispinose pygidium of pseudagnostid type is present in the *Elvinia* Zone assemblages of Cherry Creek, Egan Range, Nevada, U.S.A., USGS collection CO2527 (A. R. Palmer, pers. comm.).

Age and distribution. Late Cambrian: late *Olenus* Zone, Warwickshire, U.K.; early Franconian, *Elvinia* Zone, Nevada, U.S.A.

Comments. The generic name *Sulcatagnostus* was erected by Kobayashi (1937*a*, p. 451) for *Agnostus securiger* (see below). Apart from its possession of a third, sagittal, pygidial spine, *Sulcatagnostus securiger* (Lake) compares well with members of the *cyclopyge* group such as *Pseudagnostus ampullatus* Öpik and *P. idalis* Öpik, both of which have similar over-all morphology.

B. PAPILIONATE SPECIES GROUPS

Clarki group (Shergold 1975, p. 60) (Pl. 15, figs. 14–15)

Nominal species. **Pseudagnostus* (*Plethagnostus*) *clarki* Kobayashi, 1935*a*, p. 47, pl. IX, figs. 1–2, holotype pygidium USNM 93062, paratype USNM 146887, late Cambrian '*Briscoia*' fauna, Hard Luck Creek, Alaska; refigured Palmer 1968, p. 29, pl. 15, figs. 10, 13–14.

Diagnosis. Cephalon subovoid to subcircular, effaced, wide borders with non-deliquiate marginal furrows, papilionate, V-form anterolateral glabellar furrows, median preglabellar furrow externally effaced, present parietally. Pygidium subovoid, effaced, wide borders with non-deliquiate marginal furrows, non-plethoid, weakly deuterolobate, small posterolateral spines sited well in advance of a transverse line drawn across the rear of the deuterolobe, nine to ten axial metameres.

Other species

**Pseudagnostus clarki maximus* Shergold, 1975, pp. 70–71, pl. 5, figs. 1–2, holotype cephalon CPC 11587, paratype CPC 11588.

**Pseudagnostus clarki patulus* Shergold, 1975, pp. 62–64, pl. 1, figs. 1–6, pl. 2, figs. 1–2, holotype cephalon CPC 11524, paratypes CPC 11525–11531.

**Pseudagnostus clarki prolatus* Shergold, 1975, pp. 64–69, pl. 3, figs. 1–6, pl. 4, figs. 1–6, holotype cephalon CPC 11532, paratypes CPC 11533–11542.

**Pseudagnostus cyclopygeformis* (Sun) *sensu* Kobayashi, 1933, pp. 97–98, pl. IX, figs. 19, 23–24, pl. X, fig. 7; 1935*b*, pp. 111–112, pl. III, figs. 12–14, IGUT no numbers.

**Pseudagnostus elix* Shergold, 1975, pp. 71–73, pl. 2, figs. 3–7, holotype pygidium CPC 11688, paratypes CPC 11689–11691.

**Pseudagnostus laevis* Palmer, 1955, pp. 97–98, pl. 19, figs. 8–9, 11–12, holotype pygidium USNM 123559, paratypes USNM 26990, 123560–123561.

**Pseudagnostus orbiculatus* Shergold, 1975, pp. 73–74, pl. 12, figs. 8–12, holotype cephalon CPC 11591, paratypes CPC 11592–11595.
**Pseudagnostus papilio* (*pars*) Shergold, 1972, pp. 28–31, pl. 1, fig. 2, CPC 8443, *non* pl. 1, figs. 1, 3–8, pl. 2, figs. 1–2 [*convergens* group].
**Peronopsis planulata* Raymond, 1924, p. 395, pl. 12, fig. 9, holotype pygidium MCZ 1729.
**Pseudagnostus* cf. *prolongus* (Hall and Whitfield) *sensu* Kindle and Whittington, 1965, p. 686, pl. 1, figs. 17–20, Kindle Collection.
**Pseudagnostus* sp. *II*, Shergold 1972, p. 35, pl. 2, figs. 6–7, CPC 8458–8459.
**Pseudagnostus* sp. *III*, Shergold 1972, pp. 35–36, pl. 2, fig. 8, CPC 8460.
**Pseudagnostus* sp., Robison and Pantoja-Alor 1968, p. 780, pl. 97, figs. 17–18, USNM 158884–158885.

Possibly also belonging to this species group are:

Pseudagnostus α sp., Kobayashi 1935*a*, p. 41, plus plate explanation, pl. VIII, fig. 3, repository and number not known.
Pseudagnostus β sp., Kobayashi 1935*a*, p. 41, plus plate explanation, pl. VIII, fig. 4, repository and number not known.

Age and distribution. Late Cambrian: pre-Payntonian and Payntonian, *Rhaptagnostus clarki patulus* with *Caznaia squamosa* through *Neoagnostus quasibilobus* with *Tsinania nomas* Assemblage-Zones (Shergold 1975), western Queensland, Australia; Trempealeauan *Saukia* Zone, *Saukiella pyrene*? and *S. serotina* Subzones, Nevada, Montana, Vermont, Alaska, U.S.A.; Trempealeauan?, Oaxaca Province, Mexico; late Changshanian, *Kaolishania* Zone, Shantung, China; Fengshanian, *Tsinania* Zone, North and South Korea.

Comments. The *clarki* group is a homogeneous association of taxa exhibiting specific and subspecific variation in shapes and proportions, and border parameters.

Convergens group (Shergold 1975, p. 74) (Pl. 16, figs. 1–2)

Nominal species. **Pseudagnostus convergens* Palmer, 1955, pp. 96–97, pl. 19, figs. 14–15, holotype pygidium USNM 123562, paratype USNM 123563, late Cambrian, Trempealeauan, *Saukia* Zone, *Saukiella pyrene* Subzone, Nevada, U.S.A.

Diagnosis. Cephalon subovoid to subcircular, effaced and partially effaced, narrow borders with non-deliquiate marginal furrows, papilionate, V-form anterolateral furrows, median preglabellar furrow externally effaced, present parietally. Pygidium subovoid, with rearwards converging flanks and acrolobe, narrow borders with non-deliquiate marginal furrows, subplethoid, weakly deuterolobate, very small posterolateral spines well in advance of a transverse line drawn across the rear of the deuterolobe, ten late holaspid metameres.

Other species

**Pseudagnostus bifax* Shergold, 1975, pp. 75–79, pl. 9, figs. 1–7, holotype cephalon CPC 11596, paratypes CPC 11597–11602, 11649, 11656, 11662, 11667–11668.
Agnostus cyclopygeformis Sun, 1924, pp. 26–28, pl. II, fig. 1*a–h*, GSCh 501–504, 507–510; 1935, p. 16, pl. III, figs. 29–32, NUP 1194–1197; also **Pseudagnostus cyclopygeformis* (Sun) *sensu* Endo, 1939, p. 6, pl. 1, figs. 14–15, USNM 96092b–c, *non* fig. 13, USNM 96092a; *P. cyclopygeformis* (Sun) *sensu* Lu *et al.*, 1957, pl. 137, figs. 20–21, repository and numbers not known; 1965, p. 42, pl. 4, figs. 9–12, repository and numbers not known.
Pseudagnostus obsoletus Lermontova, 1951, pp. 10–11, pl. 2, figs. 8–10, repository and numbers unknown.
Pseudagnostus cf. *obsoletus* Lerm. (MS), Lermontova, 1940, p. 125, pl. 49, fig. 11, repository and number not known.
**Pseudagnostus papilio* Shergold, 1972, pp. 28–31, pl. 1, figs. 1, 3–8, *non* fig. 2 [*clarki* group], pl. 2, figs. 1–2, holotype cephalon CPC 8442, paratypes CPC 8443–8450; also 1975, pp. 79–82, pl. 11, figs. 1–8, CPC 11669–11677.

Possibly also belonging to this group is:

**Pseudagnostus* sp. *I*, Shergold 1972, p. 34, pl. 2, figs. 3–5, CPC 8457.

Age and distribution. Late Cambrian: pre-Payntonian, *Rhaptagnostus bifax* with *Neoagnostus denticulatus* and *R. clarki maximus* with *R. papilio* Assemblage-Zones (Shergold 1975), western Queensland, Australia; late Changshanian, *Kaolishania* Zone, Shantung, Hopei, China; Trempealeauan, *Saukiella* pyrene Subzone, *Saukia* Zone, Nevada, U.S.A.; Shidertan, *Lotagnostus trisectus*/*Peltura* Zone, Kazakhstan, U.S.S.R.

Comments. As for *clarki* group.

PSEUDAGNOSTID SPECIES UNASSIGNED

**Pseudagnostus* cf. *P. convergens* Palmer *sensu* Lochman, 1964, p. 51, pl. 13, fig. 10, USNM 140686.

Agnostus cyclopyge Tullberg *sensu* Sun, 1935, pp. 15–16, pl. III, figs. 33–36, THU 1198–1201; *sensu* Lu *et al.* 1965, pp. 40–41, pl. 4, figs. 1–2 [reproductions of Sun's figures].

Pseudagnostus cyclopyge (Tullberg) *sensu* Wilson, 1954, p. 284, pl. 25, fig. 19, pl. 26, fig. 13.

*?*Hypagnostus empozadensis* Rusconi, 1953, p. 6 [*nom. nud.*]; 1954, pp. 34–35, pl. II, fig. 11, NHMM 16872, an effaced papilionate subquadrate cephalon.

**Leiopyge empozadense* Rusconi, 1953, pp. 5–6 [*nom. nud.*]; 1954, pp. 33–34, pl. II, fig. 10, NHMM 16856, an incomplete pygidium.

**Oedorhachis greendalensis* Resser, 1938, p. 51, pl. 10, fig. 9, USNM 94861.

**Plethagnostus gyps* Clark, 1923, p. 124, pl. 1, fig. 9, holotype pygidium MCZ 1700; refigured Clark, 1924, p. 16, pl. 3, fig. 2; *sensu* Rasetti, 1944, p. 234, pl. 36, figs. 20–22, LU 1105a–c [may represent a distinct *en grande tenue* papilionate species group].

Pseudagnostus impressus Lermontova, 1940, p. 125, pl. 49, fig. 13, 13*a*, repository and numbers not known.

**Pseudagnostus jeholensis* Kobayashi, 1951, pp. 76–77, pl. 7, figs. 13–14, IGUT no numbers; reproduced *in* Lu *et al.* 1965, p. 43, pl. 4, figs. 16–17.

Pseudagnostus josepha (Hall) as illustrated by: Frederickson 1949, p. 362, pl. 72, fig. 17, OGM 105-16F-53; Lochman 1950, pp. 329–330, pl. 46, fig. 14; Nelson 1951, p. 776, pl. 107, fig. 5; Bell *et al.* 1952, pp. 196–197, pl. 32, fig. 4*a*–*b*, pl. 33, fig. 1; Ellinwood 1953, p. 65, pl. 4, figs. 9–10; Wilson 1954, p. 284, pl. 25, figs. 5, 22.

**Agnostus maladensis* Meek, 1873, p. 464, USNM 24597 [a medley of taxa].

**Pseudagnostus mesleri* (Resser) *sensu* Lochman, 1940, pp. 26–27, pl. 2, figs. 38–43, USNM 98703.

Microdiscus paronai Airaghi, 1902, p. 23, pl. 2, figs. 24–25, repository and numbers not known.

**Spinagnostus pedrensis* Rusconi, 1951, pl. 8, fig. 9, NHMN 9963 [referred to *Leiopyge* by Rusconi 1953, p. 6, originally illustrated as a cephalon, this specimen is actually an indeterminate pseudagnostid pygidium].

Agnostus pii Airaghi, 1902, p. 19, pl. 1, fig. 28, repository and number not known.

**Pseudagnostus prolongus* (Hall and Whitfield) *sensu* Palmer, 1960, p. 61, pl. 4, figs. 5–6, USNM 136833a–b.

Pseudagnostus (*Rhaptagnostus*?) *semiovalis* Kobayashi, 1937*a*, pp. 452–453, pl. II, figs. 8–9, repository Freiburg, types destroyed (Kobayashi pers. comm., 1972).

?*Pseudagnostus* sp., Lu 1956*a*, pp. 282–283, pl. 1, fig. 8; Lu *et al.* 1965, p. 44, pl. 4, fig. 20, repository and number not known.

PSEUDAGNOSTI *NOMINA NUDA*

Pseudagnostus ovatus Rusconi, 1950, p. 94 [plate explanation error, fig. 6, for *P. parabolicus*].

Pseudagnostus huangluoensis Kobayashi, 1951, p. 75.

Pseudagnostus mirus Pokrovskaya *in* Vasilenko, 1963, p. 22, Chart 3 [listed].

Pseudagnostus solus Endo *in* Endo and Resser, 1937, p. 304 [listed].

DEFINITION OF GENERIC GROUPS

Since Jaekel erected *Pseudagnostus* in 1909 several attempts have been made to subdivide the genus, e.g. Clark 1923, Whitehouse 1936, Kobayashi 1937*a*, 1955, Lermontova 1940, *inter alia*. Accordingly there is a proliferation of generic and subgeneric names, some of which have doubtful taxonomic validity. These are briefly reviewed below in discussing the generic classification of pseudagnosti.

In this classification *Pseudagnostus* Jaekel, 1909, type species *Agnostus cyclopyge* Tullberg, 1880 (p. 26, pl. II, fig. 15*a*, *c*), is restricted to include only the *cyclopyge*, *communis*, and *bulgosus* species groups as documented above.

Plethagnostus, erected by Clark (1923, p. 124), originally differentially diagnosed from *Pseudagnostus* by having 'divergent dorsal [accessory] furrows continued to the border of the pygidium' as in *Plethagnostus gyps* Clark (1923, pl. I, fig. 9), its type species, is suppressed. This action is taken because:

Many pseudagnostid species are plethoid, the courses of the accessory furrows continuing to the marginal furrows, particularly in *en grande tenue* and partially effaced species groups, e.g. the *cyclopyge* and *communis* group referred above to *Pseudagnostus*; the type species is based on a single incomplete pygidium (MCZ 1700) which lacks a posterior margin; and usage of the name *Plethagnostus* has been confused by Kobayashi (1935*a*, pp. 46–47), who utilized Clark's taxon in a subgeneric sense for the species *Pseudagnostus clarki*, which has a papilionate cephalon and non-plethoid pygidium with effaced accessory furrows! Subsequent usage of *Plethagnostus* appears to have followed Kobayashi's interpretation. It is recommended that this practice be discontinued because the type specimen of *P. gyps* quite obviously does not belong to the same species group as *Pseudagnostus clarki*, and because of its incompleteness cannot be adequately classified anyway. *Plethagnostus gyps* Clark is left unclassified with respect to species groups and is referred to *Pseudagnostus s.l.*

Rhaptagnostus Whitehouse (1936, p. 97), based on *A. cyclopygeformis* Sun, 1924, was differentiated from *Pseudagnostus* by possessing 'an elliptical arrangement of foramina [notulae] in the post-axial region' of the pygidium, and a 'simple, non-spinose brim'. Sun's specimens (1924, pl. II, fig. 1*a*–*h*) appear to be parietal surfaces, and such surfaces of many pseudagnosti display notular lines given the right medium of preservation. The absence of pygidial spines in any pseudagnostid species is greatly doubted. Very often these spines are extremely small and readily destroyed by certain modes of preservation, e.g. in arenaceous matrices, and by negligent preparation. Cephala matched by Sun with the pygidia which Whitehouse chose to differentiate from *Pseudagnostus*, are papilionate and thus different from those of *P. cyclopyge* (Tullberg), which is spectaculate. *P. cyclopygeformis* (Sun) is here included within the *convergens* species group. *Rhaptagnostus* is used herein to distinguish the two closely related papilionate species groups, *clarki* and *convergens*, from spectaculate ones at the generic level. This name is preferred to the previously and erroneously used *Plethagnostus* Clark *sensu* Kobayashi 1935*a*.

Sulcatagnostus was erected by Kobayashi (1937*a*, p. 451) for *A. securiger* Lake (1906, p. 20, pl. II, fig. 11), and distinguished by possessing 'irregular divergent furrows on the side lobes' (Kobayashi, 1937*a*, pp. 450–451). This was later redefined as 'Pseudagnostinae with reticulated furrows on side lobes' (Kobayashi 1939, p. 159). The reticulation described (Pl. 15, fig. 13) refers to the caecal network of the cephalic acrolobe and pygidial pleural lobes. The presence of a caecal display, common on exfoliated specimens and thin exoskeletons under certain conditions of preservation, is itself insufficient to justify differentiation from *Pseudagnostus*. Overlooked by Kobayashi, however, is the fact that *A. securiger* Lake also possesses a trispinose pygidium (Rushton *in* Taylor and Rushton 1971, p. 20), which certainly is a significant characteristic. In view of the otherwise similar morphology to spectaculate pseudagnosti, *Sulcatagnostus* is retained as a subgenus of *Pseudagnostus*.

Euplethagnostus Lermontova (1940, p. 126), based on *E. subangulatus* Lermontova (1940, pl. XLIX, fig. 15, 15*a*), was compared to *Plethagnostus* Clark, 1923, but distinguished by the possession of posterolateral pygidial spines, sometimes an intranotular axis (lanceolate ridge), and the presence of a posterior pygidial terminal node. Such characteristics are emphatically not diagnostic in generic classification because: the type specimen of *P. gyps*, type species of *Plethagnostus*, is damaged and it is not possible to ascertain whether it possessed spines—Clark (1923) assumed that their traces were still apparent, and Rasetti (1944, pl. 36, figs. 20–22) has illustrated material possessing pygidial spines which can be assigned to *P. gyps*; the presence of terminal nodes and intranotular axes is commonly observed on a multiplicity of pseudagnostid parietal surfaces; and Lermontova's specimens are poorly illustrated and inadequately described, no type specimen was selected for *E. subangulatus* and the repository of material is unknown. *E. subangulatus* appears most similar to species classified herein with the *clavus* group. Its type specimens require redescription and re-illustration if the name *Euplethagnostus* is to be retained.

Problems associated with the taxonomic validation of *Pseudorhaptagnostus* Lermontova (1940, p. 126) have been previously discussed (Shergold 1972, p. 28). These problems remain unresolved. The name *Pseudorhaptagnostus* was introduced by Lermontova in 1940, *P. simplex* Lermontova (1951, pp. 12–13, pl. 2, figs. 11–17) being designated as type species. Although a second species, *P. punctatus* Lermontova, was illustrated in 1940, *P. simplex* was neither illustrated nor described until 1951. At this time a heterogeneous collection of cephala and pygidia was figured. While the pygidia (Lermontova 1951, pl. 2, figs. 11–14) show morphological consistency, two types of cephalon were figured: one (fig. 15) is probably that associated with the pygidia, whereas the others (figs. 16–17) belong to a species of the *convergens* group. Nikitin (1956, pl. XIV, figs. 4–5) re-illustrated this combination of *convergens* group cephalon with *Pseudorhaptagnostus* pygidium. Such mismatching appears to result directly from Lermontova's failure to designate a holotype. According to Lermontova (1940), *Pseudorhaptagnostus* is differentiated from *Rhaptagnostus* Whitehouse in possessing a thickened pygidial rim and well-developed posterolateral spines. A lanceolate field [intranotular axis] is stated to be present on pygidial internal casts [parietal surfaces]. None of these characteristics is considered to justify separation from *Pseudagnostus*, either separately or in combination. Other characteristics exhibited by *Pseudorhaptagnostus simplex* can, however, be utilized if the name is to be retained (Shergold 1972, p. 28). These, which can only be verified from examination of the actual material on which *Pseudorhaptagnostus* is based, involve the cephalic and pygidial shapes, nature of their borders and pygidial spines, and pygidial segmentation. Although it appears that *P. simplex* has much in common with the *clavus* species group recognized above, judgement on the validity of the genus must await clarification of the concept of the taxon. It is very likely that *Pseudorhaptagnostus* and *Euplethagnostus* Lermontova are synonyms. If so, *Pseudorhaptagnostus* has priority, being first listed.

Neoagnostus Kobayashi (1955, p. 473), type species *N. aspidoides* Kobayashi (1955, pp. 473–474), possesses a cephalon with trilobed glabella and median preglabellar furrow (Pl. 16, fig. 16). The holotype cephalon (Kobayashi 1955, pl. VII, fig. 5) is a parietal mould preserved *en grande tenue*. The associated pygidium (fig. 4), labelled paratype, is geragnostoid.

Hyperagnostus Kobayashi (1955, p. 474), based on *H. binodosus* Kobayashi (1955, p. 475), also has a trilobed glabella, but is said to differ from *Neoagnostus* in not possessing a median preglabellar furrow (Pl. 16, fig. 17). The holotype cephalon (1955, pl. VII, fig. 2) is partially exfoliated, somewhat distorted, and incomplete, the anterior portion of the cephalon having been lost. A thin veneer of exoskeleton lies across the position in which the median preglabellar furrow would be expected and its presence or absence cannot be absolutely verified; it appears not to be present on the external surface, but may be weakly present on the parietal surface. The assigned pygidium (1955, fig. 3) is agnostoid rather than pseudagnostoid. Although *Neoagnostus* and *Hyperagnostus* occur at different localities and are of slightly different ages, they are temporarily synonymized herein, *Neoagnostus* taking priority.

Machairagnostus Harrington and Leanza (1957, p. 63), based on *M. tmetus* Harrington and Leanza (1957, p. 64, fig. 7), is represented by parietal surfaces. The glabella is faintly trisegmented, but the cephalic acrolobe is scrobiculate. The pygidium is weakly deuterolobate, and the muscle-scar impressions of the third axial segment are incorporated into the anterior portion of the axis which is delineated by axial furrows. *M. tmetus* has the glabellar morphology of members of the *araneavelatus* species group, and pygidial characteristics of the *bilobus* group with which it is classified here. The scrobiculation of the cephalic acrolobe is non-diagnostic under the conditions of this classification, and so *Machairagnostus* is synonymized with *Neoagnostus*.

Pseudagnostina Palmer (1962, pp. 20–21), type species *P. contracta* Palmer (1962, pp. 20–21, pl. 2, figs. 18–20, 22–25), was coined for pseudagnosti having '*Peronopsis*-like cephalon and *Pseudagnostus*-like pygidium'. The concept of the taxon is broadened somewhat here by the inclusion of some Asian species previously referred to *Agnostus douvillei* Bergeron, 1899. Because of over-all basic similarity of the pygidium to that of other pseudagnosti, *Pseudagnostina* is regarded here as a subgenus of *Pseudagnostus*—effaced and partially effaced, strongly spectaculate, weakly deuterolobate species constituting the *contracta* species group.

SUMMARY

Spectaculate species groups fall readily into two larger groupings:

1. The *bulgosus–communis–contracta–cyclopyge–securiger* grouping whose morphology differs by degree and which can largely be encompassed within a concept of *Pseudagnostus* based on its type species *P. cyclopyge* (Tullberg 1880). Effaced

variants are differentiated as the *contracta* group regarded as a distinct subgenus, *Pseudagnostina* Palmer, 1962; and the *securiger* group, with three pygidial spines, likewise is separated at the subgeneric level as *Sulcatagnostus* Kobayashi, 1937*a*.

2. The *araneavelatus–bilobus–canadensis–clavus* grouping is united by an arrangement of glabellar lobation and furrowing different from that of *Pseudagnostus*. The anterolateral lobes are closer together and may meet adaxially so that the glabellar furrows intersect as a cross. Within this division species groups are differentiated by shield shape, and degree of effacement, particularly by which glabellar furrows are effaced and which are not. Five generic names appear to be available for classifying these groups: *Pseudorhaptagnostus* Lermontova, 1940; *Euplethagnostus* Lermontova, 1940; *Neoagnostus* Kobayashi, 1955; *Hyperagnostus* Kobayashi, 1955; and *Machairagnostus* Harrington and Leanza, 1957. As indicated above, *Pseudorhaptagnostus* and *Euplethagnostus* may be synonyms, the former taking priority; and *Hyperagnostus* and *Machairagnostus* are regarded as synonyms of *Neoagnostus*.

Although *Pseudorhaptagnostus* and *Euplethagnostus* have priority over *Neoagnostus*, their concepts are very poorly understood, and it has been found not possible to obtain adequate information to verify their characteristics. Accordingly, *Neoagnostus* is temporarily adopted in this classification, in preference to either of the Russian genera, for the *araneavelatus–bilobus–canadensis–clavus* grouping.

The papilionate species groups, *clarki* and *convergens*, are placed here in *Rhaptagnostus* Whitehouse, 1936, because its interpretable type species is representative of the *convergens* group.

Thus the following classification is adopted:

Family Diplagnostidae Whitehouse, 1936, emend. Öpik, 1967.
Subfamily Pseudagnostinae Whitehouse, 1936.

Genus *Pseudagnostus* Jaekel, 1909.
Type species: *Agnostus cyclopyge* Tullberg, 1880 (designated Jaekel, 1909). Pseudagnostinae with long (sag.) anteriorly rounded or pointed anterior glabellar lobe, axial node lying behind anterolateral lobes and anterior furrow which is straight or curved rearwards sagittally. Shields are subcircular to subovoid, effaced to *en grande tenue*, non-deliquiate to deliquiate, weakly to strongly deuterolobate. Up to eight late holaspid pygidial metameres.

Subgenus *Pseudagnostus* Jaekel, 1909.
Type species and diagnosis as above.
Group *bulgosus*, based on *Pseudagnostus bulgosus* Öpik, 1967.
Group *communis*, based on *Agnostus communis* Hall and Whitfield, 1877.
Group *cyclopyge*, based on the type species.

Subgenus *Pseudagnostina* Palmer, 1962.
Type species: *Pseudagnostina contracta* Palmer, 1962 (by original designation). Spectaculate Pseudagnostinae with subquadrate shields and with effaced median preglabellar furrow, accessory furrows, and deuterolobe.
Group *contracta*, based on the type species.

Subgenus *Sulcatagnostus* Kobayashi, 1937*a*.
Type species: *Agnostus securiger* Lake, 1906 (designated Kobayashi, 1937*a*). Spectaculate *en grande tenue* Pseudagnostinae with trispinose pygidium.
Group *securiger*, based on the type species.

Genus *Neoagnostus* Kobayashi, 1955.
Type species: *Neoagnostus aspidoides* Kobayashi, 1955 (by original designation). Spectaculate Pseudagnostinae with anterolateral glabellar lobes close together or meeting adaxially, and a tendency to efface or over-deepen either the furrows in front of or behind the anterolateral lobes; anterior lobe small and rhomboid. Pygidium with distinct tendency to incorporate a third segment into that portion of the axis defined by axial furrows; retral spines. Generally, species have subquadrate shields, whose external morphology may be effaced, partially effaced or *en grande tenue*, non-deliquiate to deliquiate, weakly to strongly deuterolobate. Up to eight late holaspid pygidial metameres.
Group *araneavelatus*, based on *Pseudagnostus araneavelatus* Shaw, 1951.
Group *bilobus*, based on *Pseudagnostus bilobus* Shaw, 1951.
Group *canadensis*, based on *Agnostus canadensis* Billings, 1860.
Group *clavus*, based on *Pseudagnostus clavus* Shergold, 1972.

Genus *Rhaptagnostus* Whitehouse, 1936.
Type species: *Agnostus cyclopygeformis* Sun, 1924 (designated Whitehouse, 1936). Papilionate Pseudagnostinae with subovoid shields, externally generally effaced or partially effaced. Pygidia with ten late holaspid metameres; spines advanced with respect to the rear of the deuterolobe, and minute.
Group *clarki*, based on *Pseudagnostus clarki* Kobayashi, 1935*a*.
Group *convergens*, based on *Pseudagnostus convergens* Palmer, 1955.

Non-investigated genera of Pseudagnostinae are *Litagnostus* Rasetti, 1944, *Xestagnostus* Öpik, 1967, and *Oxyagnostus* Öpik, 1967.

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J. H. SHERGOLD

Bureau of Mineral Resources
P.O. Box 378
Canberra
A.C.T. 2601
Australia

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APPENDIX A

MORPHOLOGICAL CONDITIONS APPLICABLE TO PSEUDAGNOSTI

Constricted/unconstricted acrolobes. If the lateral margins of the acrolobe are curved slightly inwards, then the condition is known as constricted (Öpik 1967). Where a constant curvature of the flanks of the acrolobe is maintained the condition is said to be unconstricted. Most species of *Pseudagnostus* have constricted pygidial acrolobes, the condition being most readily observed on parietal surfaces. Some species also have constricted cephalic acrolobes.

Deliquiate/non-deliquiate marginal furrows. Marginal furrows which are deeply grooved or channel-like are described as deliquiate (Shergold 1975). If the marginal furrow is merely a break in convexity at the junction of the acrolobe and border the condition exhibited is non-deliquiate. Gradations exist, for which the term subdeliquiate is introduced to permit the description of degrees of deepening of furrows. Degree of deliquiation is related directly to degree of effacement. Exoskeleton and mould of the same specimen will have differing degrees of deliquiation, the mould having deeper, wider furrows.

Deuterolobate. All pseudagnosti are deuterolobate. Degree of elevation of the deuterolobe, however, varies. *En grande tenue* species generally have a tumid deuterolobe well defined by accessory furrows. For this condition the term strongly deuterolobate is used here. Species with depressed deuterolobes are described as weakly deuterolobate.

Effaced/effacement/partial effacement. An effaced condition is one in which furrows and lobes with visible convexity are obliterated to give a smooth or nearly smooth surface. In Pseudagnostinae all conditions of partial effacement exist, from highly effaced to *en grande tenue*.

En grande tenue. Introduced by Öpik (1961*b*, p. 55), this term was redefined (Öpik 1967, p. 56) to categorize agnostids having distinct lobes and furrows.

Papilionate. Pseudagnostinae in which the axial glabellar node lies between the anterolateral lobes are termed papilionate. The term is derived from the butterfly-like appearance of these lobes and furrows (Shergold 1975, p. 42).

Plethoid. Pseudagnostinae with accessory furrows clearly encircling the deuterolobe or continued posteriorly to the marginal furrow exhibit a plethoid condition (Shergold 1972, p. 15).

Retral. This term refers to the siting of the posterolateral pygidial spines at the rear of the shield, behind or at the level of the rear of the deuterolobe.

Simplicimarginate/zonate borders. Simplicimarginate agnostids have a basic unmodified border. Those having a duplicated posterior margin are said to be zonate (Öpik 1967, p. 61).

Spectaculate. A term introduced for pseudagnosti in which the axial glabellar node lies to the rear of the anterolateral glabellar lobes, and is therefore also to the rear of the anterior glabellar furrow. The resulting appearance resembles a bespectacled face—hence the term (Shergold 1975, p. 42).

APPENDIX B

Classification of Species Assignable to *Pseudagnostus* sensu lato

Species/Author/Date	Original Generic Assessment	Species Group	Revised Generic Assignment
1. *acutifrons* Troedsson, 1937	*Rhaptagnostus*	*clavus*	*Neoagnostus*
2. cfr. *acutus* Kobayashi, 1938	*Homagnostus*	*clavus*?	*Neoagnostus*
3. *ampullatus* Öpik, 1967	*Pseudagnostus*	*cyclopyge*	*Pseudagnostus* (*Pseudagnostus*)
4. *angustilobus* Ivshin, 1956	*Pseudagnostus*	*cyclopyge*	*Pseudagnostus* (*Pseudagnostus*)
5. *araneavelatus* Shaw, 1951	*Pseudagnostus*	*araneavelatus*	*Neoagnostus*
6. *aspidoides* Kobayashi, 1955	*Neoagnostus*	*bilobus*	*Neoagnostus*
7. *bifax* Shergold, 1975	*Pseudagnostus*	*convergens*	*Rhaptagnostus*
8. *bilobus* Shaw, 1951	*Pseudagnostus*	*bilobus*	*Neoagnostus*
9. *binodosus* Kobayashi, 1955	*Hyperagnostus*	*bilobus*	*Neoagnostus*
10. *bituberculatus* Ivshin, 1960	*Pseudagnostus*	*clavus*?	*Neoagnostus*
11. *boltonensis* Resser, 1938	*Oedorhachis*	*bulgosus*	*Pseudagnostus* (*Pseudagnostus*)
12. *bulgosus* Öpik, 1967	*Pseudagnostus*	*bulgosus*	*Pseudagnostus* (*Pseudagnostus*)
13. *canadensis* Billings, 1860	*Agnostus*	*canddensis*	*Neoagnostus*
14. *cavernosus* Rosova, 1960	*Pseudagnostus*	*clavus*	*Neoagnostus*
15. *chinensis* Dames, 1883 (*pars*)	*Agnostus*	*cyclopyge*	*Pseudagnostus* (*Pseudagnostus*)
16. *clarki* Kobayashi, 1935*a*	*Plethagnostus*	*clarki*	*Rhaptagnostus*
17. *clarki patulus* Shergold, 1975	*Pseudagnostus*	*clarki*	*Rhaptagnostus*
18. *clarki prolatus* Shergold, 1975	*Pseudagnostus*	*clarki*	*Rhaptagnostus*
19. *clarki maximus* Shergold, 1975	*Pseudagnostus*	*clarki*	*Rhaptagnostus*
20. *clavus* Shergold, 1972	*Pseudagnostus*	*clavus*	*Neoagnostus*
21. *coloradoensis* Shumard, 1961	*Agnostus*	*communis*	*Pseudagnostus* (*Pseudagnostus*)
22. *communis* Hall and Whitfield, 1877	*Agnostus*	*communis*	*Pseudagnostus* (*Pseudagnostus*)

Species/Author/Date	Original Generic Assessment	Species Group	Revised Generic Assignment
23. *contracta* Palmer, 1962	*Pseudagnostina*	*contracta*	*Pseudagnostus* (*Pseudagnostina*)
24. *convergens* Palmer, 1955	*Pseudagnostus*	*convergens*	*Rhaptagnostus*
25. *convexus* Chu, 1959 (*pars*)	*Homagnostus*	*cyclopyge*	*Pseudagnostus* (*Pseudagnostus*)
26. *coronatus* Shergold, 1975	*Pseudagnostus*	*araneavelatus*	*Neoagnostus*
27. *cyclopyge* Tullberg, 1880	*Agnostus*	*cyclopyge*	*Pseudagnostus* (*Pseudagnostus*)
28. *cyclopygeformis* Sun, 1924	*Agnostus*	*convergens*	*Rhaptagnostus*
29. *cyclostigma* Raymond, 1924	*Phalacroma*	*araneavelatus*	*Neoagnostus*
30. *denticulatus* Shergold, 1975	*Pseudagnostus*	*araneavelatus*	*Neoagnostus*
31. *douvillei* Bergeron, 1899	*Agnostus*	*contracta*	*Pseudagnostus* (*Pseudagnostina*)
32. *elix* Shergold, 1975	*Pseudagnostus*	*clarki*	*Rhaptagnostus*
33. *empozadense* Rusconi, 1954	*Lejopyge*	?	?
34. *empozadensis* Rusconi, 1954	*Hypagnostus*?	?	?
35. *greendalensis* Resser, 1938	*Oedorhachis*	?	?
36. *gyps* Clark, 1923	*Plethagnostus*	?	?
37. *huangliuoensis* Kobayashi, 1966	*Pseudagnostus*		nomen nudum
38. *idalis* Öpik, 1967	*Pseudagnostus*	*cyclopyge*	*Pseudagnostus* (*Pseudagnostus*)
39. *impressus* Lermontova, 1940	*Pseudagnostus*	*communis*	*Pseudagnostus* (*Pseudagnostus*)
40. *janei* Clark, 1923	*Agnostus*	*canadensis*	*Neoagnostus*
41. *jarillensis* Rusconi, 1953	*Plethagnostus*	*cyclopyge*	*Pseudagnostus* (*Pseudagnostus*)
42. *jeholensis* Kobayashi, 1951	*Pseudagnostus*	?	?
43. *josepha* Hall, 1863	*Agnostus*	*communis*	*Pseudagnostus* (*Pseudagnostus*)
44. *kobayashii* Wolfart, 1974	*Pseudagnostus*	*cyclopyge*?	*Pseudagnostus* (*Pseudagnostus*)
45. *koerferi* Monke, 1903	*Agnostus*	*contracta*	*Pseudagnostus* (*Pseudagnostina*)
46. *laevis* Palmer, 1955	*Pseudagnostus*	*clarki*	*Rhaptagnostus*
47. *latus* Kobayashi, 1938	*Pseudagnostus*	*communis*	*Pseudagnostus* (*Pseudagnostus*)
48. *leptoplastorum* Westergård, 1944	*Pseudagnostus*	*cyclopyge*	*Pseudagnostus* (*Pseudagnostus*)
49. *levatus* Romanenko, 1967	*Pseudagnostus*	*bulgosus*	*Pseudagnostus* (*Pseudagnostus*)
50. *longicollis* Kobayashi, 1966	*Pseudagnostus*	*bilobus*	*Neoagnostus*
51. *maladensis* Meek, 1873	*Agnostus*	?	?
52. *marginisulcatus* Kobayashi, 1962	*Pseudagnostus*	*cyclopyge*	*Pseudagnostus* (*Pseudagnostus*)
53. *mesleri* Resser, 1938	*Oedorhachis*	*bulgosus*	*Pseudagnostus* (*Pseudagnostus*)
54. *mestus* Öpik, 1967	*Pseudagnostus*	*bulgosus*	*Pseudagnostus* (*Pseudagnostus*)
55. *mirus* Pokrovskaya, 1963	*Pseudagnostus*		nomen nudum
56. *neon* Hall and Whitfield, 1877	*Agnostus*	*communis*	*Pseudagnostus* (*Pseudagnostus*)
57. *nganasanicus* Rosova, 1964	*Pseudagnostus*	*bulgosus*	*Pseudagnostus* (*Pseudagnostus*)
58. *nuperus* Whitehouse, 1936	*Pseudagnostus*	*cyclopyge*	*Pseudagnostus* (*Pseudagnostus*)
59. *obsoletus* Lermontova, 1951	*Pseudagnostus*	*convergens*	*Rhaptagnostus*
60. *obtusus* Belt, 1868	*Agnostus*	*cyclopyge*	*Pseudagnostus* (*Pseudagnostus*)
61. *orbiculatus* Shergold, 1975	*Pseudagnostus*	*clarki*	*Rhaptagnostus*
62. *orientalis* Kobayashi, 1933	*Pseudagnostus*	*communis*	*Pseudagnostus* (*Pseudagnostus*)
63. *ovatus* Rusconi, 1950	*Pseudagnostus*		nomen nudum
64. *papilio* Shergold, 1971	*Pseudagnostus*	*convergens*	*Rhaptagnostus*
65. *paronai* Airaghi, 1902	*Microdiscus*	?	?
66. *pedrensis* Rusconi, 1951	*Spinagnostus*	?	?
67. *pii* Airaghi, 1902	*Agnostus*	?	?
68. *planulata* Raymond, 1924	*Peronopsis*	*clarki*	*Rhaptagnostus*
69. *primus* Kobayashi, 1962	*Pseudagnostus*	*cyclopyge*	*Pseudagnostus* (*Pseudagnostus*)
70. *priscus* Kobayashi, 1955	*Trinodus*	*bilobus*	*Neoagnostus*
71. *prolongus* Hall and Whitfield, 1877	*Agnostus*	*communis*	*Pseudagnostus* (*Pseudagnostus*)
72. *pseudocyclopyge* Ivshin, 1956	*Pseudagnostus*	*cyclopyge*	*Pseudagnostus* (*Pseudagnostus*)
73. *punctatus* Lermontova, 1940	*Pseudagnostus*	*clavus*	*Neoagnostus*
74. *quadratus* Lazarenko, 1966	*Pseudagnostus*	*clavus*?	*Neoagnostus*
75. *quasibilobus* Shergold, 1975	*Pseudagnostus*	*bilobus*	*Neoagnostus*
76. *rotundatus* Lermontova, 1940	*Pseudagnostus*	*communis*	*Pseudagnostus* (*Pseudagnostus*)
77. *securiger* Lake, 1906	*Agnostus*	*securiger*	*Pseudagnostus* (*Sulcatagnostus*)
78. *semiovalis* Kobayashi, 1937*a*	*Rhaptagnostus*	?	?
79. *sentosus* Grant, 1965	*Pseudagnostus*	*communis*	*Pseudagnostus* (*Pseudagnostus*)
80. *sericatus* Öpik, 1967	*Pseudagnostus*	*cyclopyge*	*Pseudagnostus* (*Pseudagnostus*)
81. *simplex* Lermontova, 1951	*Pseudorhaptagnostus*	*clavus*	*Neoagnostus*

Species/Author/Date	Original Generic Assessment	Species Group	Revised Generic Assignment
82. *solus* Endo, 1937	*Pseudagnostus*		nomen nudum
83. *subangulatus* Lermontova, 1940	*Euplethagnostus*	*clavus*	*Neoagnostus*
84. *tennesseensis* Resser, 1938	*Oedorhachis*	*cyclopyge*?	*Pseudagnostus* (*Pseudagnostus*)
85. *tmetus* Harrington and Leanza, 1957	*Machairagnostus*	*bilobus*	*Neoagnostus*
86. *vastulus* Whitehouse, 1936	*Pseudagnostus*	*cyclopyge*?	*Pseudagnostus* (*Pseudagnostus*)
87. *vicaria* Öpik, 1967	*Pseudagnostus*	*contracta*	*Pseudagnostus* (*Pseudagnostina*)
88. *vulgaris* Rosova, 1960	*Pseudagnostus*	*clavus*	*Neoagnostus*